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Foreword

The Zoological Education Trust (ZET) [Fonds pour L'Education en Zoologie (FEZ)] was founded in 1986 as a branch of the Canadian Society of Zoology (CJZ). ZET has the mission of promoting the advancement of, and public awareness of, all branches of zoological science, with emphasis on the relationship of humans to the environment and animal diversity. In pursuit of these objectives, ZET has arranged and sponsored lectures and symposia, the recent theme of which has concerned the impacts of fish introductions. In 1988, ZET sponsored a lecture at the Canadian Society of Zoology Annual Meeting by Dr. M. Ferguson on "The genetic impact of introduced fishes on native species" (Ferguson 1990), and in 1989, supported a Canada-wide lecture tour by Dr. D. Philipp – "Fish introductions: when do good intentions go bad?" (Philipp 1990). The culmination of these efforts was an invitation by Dr. M. Weisbart, then Chair of ZET, for us to organize a symposium on "The ecological and genetic implications of fish introductions (FIN)." The FIN symposium was held at the Great Lakes Institute, University of Windsor, May 17–19, 1990, following the 33rd Annual Conference of the International Association of Great Lakes Research. The current volume contains the Proceedings of the FIN symposium. In addition to support from the main sponsor, ZET, the symposium was made possible by a NSERC Conference Grant. As organizers, we wish to thank the sponsors, the participants, as well as those who aided in running the symposium. As editors, we are grateful to all those who reviewed manuscripts, and to the *Canadian Journal of Fisheries and Aquatic Sciences* for publishing this issue.

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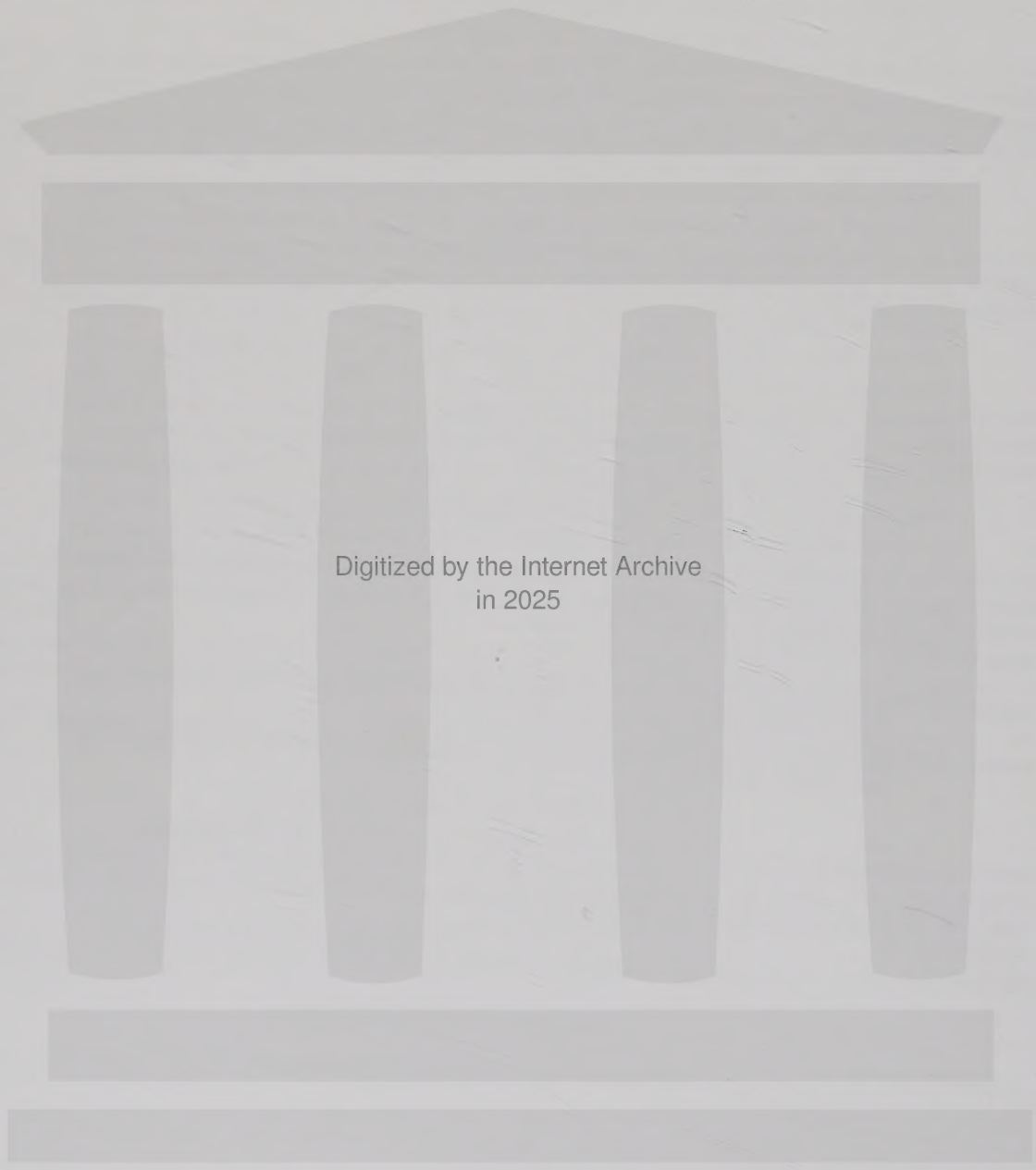

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Introduction to the International Symposium on "The Ecological and Genetic Implications of Fish Introductions (FIN)"

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In the last decade of the 19th century, North Americans recognized the need to protect and rehabitate their fisheries resources. Initial efforts were directed towards the Great Lakes, because the 10 000 commercial fishermen operating on these lakes (Smith et al. 1887) organized an effective political lobby in response to the precipitous decline in native fish stocks. The first international conference on fisheries of the Great Lakes was held in 1891 (MacCallum 1892), and at this meeting two solutions to the collapse of the fishery were proposed — the search for new species which might be introduced, and the establishment of hatcheries to enhance populations of native species.

The potential benefits of introducing exotics was enforced by some spectacular successes such as the rapid expansion of shad populations along the Pacific coast of North America following their introduction to California in 1871 (MacCallum 1892). In planning introductions there was little concern that new species might displace residents — introduced species would merely utilize incompletely exploited food resources. Enthusiasm faded when it became clear both that planned introductions rarely succeeded and that massive stocking programs often had undesirable side-effects. For example, the release of 700 000 shad in the 1870's failed to result in establishment of the species in Lake Ontario, but did lead to the inadvertent introduction of alewife which rapidly spread through the Great Lakes (Smith 1890).

The uncertain performance of introduced species saw hatcheries direct their efforts towards the supplementation of native species. There was a strong conviction that these efforts would arrest the decline in fish stocks in the Great Lakes. For example, Smith (1890) noted that "it is entirely practicable, to restore and maintain these fisheries by adequate resort to fish cultural practices." The first stocking programs were mounted by State governments, but by 1880 the U.S. Fish Commission had established its own program and within a decade was stocking 150 million whitefish fry each year, as well as walleye and lake trout. Some of the State hatcheries were themselves large scale operations — the Detroit hatchery alone released 160 million whitefish fry in 1890, derived by stripping eggs from 10 000 wild fish. Canada was less aggressive in launching stocking programs. In 1890 there was just one Federal hatchery on the Great Lakes, but two years later Ontario's Fish and Wildlife Commission recommended the establishment of Provincial hatcheries (MacCallum 1892). By this time it shoud have been clear that stocking programs had failed to rescue the fishery, but the facts were denied. The U.S. Fishery Commission report of 1892 (Smith 1892) contains perhaps the most blatant example of such denial "in nearly every lake the catch of whitefish has decreased since 1885 (in spite of stocking programs). No well informed person will argue from this that fish culture in the Great Lakes is a failure"! With a century's hindsight, it is clear that hatchery supplements failed to prevent the collapse of the Great Lakes fisheries. Indeed, as wild fish stocks disappeared the hatcheries either closed or shifted to a reliance upon fish held as broodstock. Comparing the Great Lakes fish community with that of the 1890's one is struck by the extent of faunal turnover (Regier and Hartman 1973). Unfortunately, the fate of the Great Lakes fish community is representative of the situation apparent in major water bodies around the world.

The FIN symposium aimed to provide a status report on both biological issues relating to fish introductions and to examine the regulatory framework which controls introductions in North America. The symposium differed in two important respects from preceeding meetings which have examined the impact of fish introductions (Courtenay and Stauffer 1984; DeSilva 1989). Firstly, it examined not only the impacts of the introduction of exotics, but also of stocking programs involving native species. Secondly, it did not focus exclusively on biological issues, but instead involved an examination of the regulatory framework relating to these issues.

The program provided a global perspective on the extent of fish introductions (Section 1), as well as a more detailed examination of specific fish groups in North America (Section 2). The latter papers provide a challenge to the typological species concept which has, until recently, pervaded fisheries management. In fairness, papers presented at the symposium (Section 3) made clear that methodologies to both discriminate and quantify the extent of divergence among fish stocks have only recently become available. Some of the emerging techniques for stock recognition were discussed as well as the new insights gained from their application. The ability to recognize stocks is a necessary antecedent to efforts which ensure their maintenance. The conservation of genetic diversity is now a well established goal of plant and animal husbandry (Knutson and Stoner 1989) as well as in endangered species breeding programs (Cohn 1990). The same ethos needs to be transferred to fishery management programs to ensure the maintenance of genetic diversity in fish stocks. The symposium considered both effective ways to sustain genetic diversity in an aquacultural context and the dangers inherent in the emergence of a few dominant aquaculture strains (Section 4). Other papers made clear the need to minimize the genetic impacts of hatchery fish on wild stocks. Stocking programs often involve interbasin transfers of fish, and the miscegenation resulting from such transfers may undermine the adaptation of resident stocks. Even when hatchery stocks originate locally, fish which thrive in hatcheries may be so poorly suited to life in nature that their introduction reduces the fitness of wild stocks. The problems arising from the admixture of domesticated and wild fish stocks will clearly grow in importance as a consequence of the rapid increase in escapees from aquaculture operations. The meeting also made it clear that as fishery managers act to deal with these

issues they will be confronted with new challenges associated with the introduction of genetically engineered fish.

It was evident from the meeting that the biological implications of introductions, especially those involving transfers within the natural distribution of a species, are only beginning to be appreciated. The papers examining North American regulatory programs in relation to faunal introductions indicated that they too are natal (Section 5). The multiplicity of contributions signals the parochial nature of extant programs. Yet, in the absence of biotic barriers along internal and international borders, the actions of each jurisdiction impacts upon its neighbours. The need for a binational accord is obvious, yet the primary vehicle for such co-operation, the Great Lakes Water Quality Agreement, focuses on chemical and ignores biological contaminants (IJC 1988). The recent unplanned introduction of undesirable exotics, such as the zebra mussel and ruffe, may offer a rare opportunity to generate sufficient political will to make possible new policy formulation (IJC/GLFC 1990). The FIN symposium makes clear that emerging policy needs to be sufficiently comprehensive to address the impacts arising from the release of endemic species as well as transcontinental invaders.

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(JB220)

A Global Perspective

Fish Introductions in Africa and Some of Their Implications[1]

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Ogutu-Ohwayo, R., and R. E. Hecky. 1991. Fish introductions in Africa and some of their implications. Can. J. Fish. Aquat. Sci. 48 (Suppl. 1): 8–12.

Fish introductions in Africa have been made at various spatial scales from small fish ponds to the largest lakes, primarily to sustain or increase production, though some were to develop sport fisheries and to control unwanted organisms. Some introductions have fulfilled their objective in the short term, but several "successful" introductions have created uncertainties about their long-term sustainability. *Lates niloticus, Oreochromis niloticus, O. leucostictus, Tilapia melanopleura* and *T. zilli* were introduced into Lakes Victoria and Kyoga in 1950's and early 1960's; by the 1980's *L. niloticus* and *O. niloticus* dominated the fisheries, having virtually eliminated a number of endemic species. In Lake Victoria, the loss of genetic diversity has been accompanied by a loss of trophic diversity; the transformation of the fish community coincided with profound eutrophication (algal blooms, fish kills, hypolimnetic anoxia) which might be related to alterations of the lake's food-web structure. By contrast, the introduction of a planktivore, *Limnothrissa miodon* into Lake Kivu and the Kariba reservoir has established highly successful fisheries with little effect on the pre-existing fish community or trophic ecology. The endemic species-rich African Great Lakes may be particularly sensitive to introductions. Species extinctions, introgressive hybridization and ecosystem alterations may occur following introductions.

En Afrique, l'introduction de poissons, réalisée à différentes échelles dans l'espace depuis les petits étangs de pêche jusqu'aux lacs les plus grands, a eu pour objectif principal le maintien ou l'accroissement de la production, bien que dans certains cas l'introduction ait visé l'expansion de la pêche sportive et la répression d'organismes indésirables. À court terme, quelques cas d'introduction ont été couronnées de succès, mais des doutes planent sur la durabilité à long terme du succès de plusieurs de ces «réussites». *Lates niloticus, Oreochromis niloticus, O. leucostictus, Tilapia melanopleura* et *T. zilli* ont été introduits dans les lacs Victoria et Kyoga au cours des années 50 et au début des années 60; dès les années 80, *L. niloticus* et *O. niloticus* dominaient les pêcheries et avaient pratiquement éliminé un certain nombre d'espèces endémiques. Dans le lac Victoria, la perte de diversité génétique s'est accompagnée d'une perte de diversité trophique; la transformation de la communauté de poissons a coïncidé avec une eutrophisation importante (proliférations d'algues, mortalités massives de poissons, raréfaction de l'oxygène dans l'hypolimnion) qui peut être liée aux modifications de la structure du réseau alimentaire du lac. Par contre, l'introduction d'un planctivore, *Limnothrissa miodon*, dans le lac Kivu et le réservoir Kariba a permis l'établissement d'une pêche très fructueuse sans que la communauté de poissons et l'écologie trophique originales ne soient grandement perturbées. Les Grands Lacs africains, riches en espèces endémiques, peuvent être particulièrement vulnérables à l'introduction de poissons qui peut entraîner l'extinction de certaines espèces, une hybridation introgressive et des modifications écosystémiques.

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The primary purpose of fish introductions in Africa is to maintain or increase yields, but introductions have also been conducted to establish sport fisheries and to control disease vectors. Fish is the most important source of animal protein in many African countries. Because of the high demand for fish, many native fish stocks have been depleted by overfishing. Fish introductions are often contemplated and frequently implemented in an attempt to maintain or increase yields from wild fisheries. *Lates niloticus* L. (Nile perch) and four tilapiine species; *Oreochromis niloticus* L. (Nile tilapia), *Oreochromis leucosticutus*, *Tilapia zilli*, and *Tilapia melanopleura* (*T. rendalli*) were introduced into Lakes Victoria and Kyoga during the 1950's and early 1960's (Gee 1964; Welcomme 1964, 1966). The Nile perch was introduced supposedly to feed on the small size haplochromine cichlids which were at that time abundant but not fully exploited, so as to convert them into larger table fish (Graham 1929; Worthington 1929; Anderson 1961). *Tilapia zilli* was introduced to feed on macrophytes which were not being utilized by any commercially important fish, but *O. niloticus* and *O. leucostictus* were introduced to supplement stocks of the native tilapiines which had declined due to overfishing. *Tilapia melanopleura* was introduced accidentally from fish ponds. Fish have also been introduced into reservoirs constructed for generation of electricity and for irrigation. The clupeid, *Limnothrissa miodon*, was introduced in the Kariba Reservoir to create an open water pelagic fishery

[1]This paper forms part of the Proceedings of the Ecological and Genetic Implications of Fish Introductions Symposium (FIN) convened at the Great Lakes Institute, University of Windsor, Ontario, Canada, May 17–19, 1990.

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(Spliethoff et al. 1983; Marshall 1988). This species was also introduced into Lake Kivu for the same purpose (Spliethoff et al. 1983).

The growth of fish farming has led to introduction and transfer of many fish species in Africa. Many tilapiine species have been transferred within Africa for aquaculture and other fishes like the rainbow trout and the Chinese carps have been introduced into Africa from other continents (Welcomme 1984).

The desire of the colonial administrators to have sport fisheries also led to introduction of trout, into high altitude streams, and this seems to have contributed to the urge to introduce Nile perch in Lake Victoria.

Some species, like *Gambusia affinis* and *Poecelia reticulata*, which feed on mosquito larvae have been introduced in parts of Africa to control mosquitoes which are vectors of malaria parasites, while the molluscivore *Astatoreochromis alluaudi* has been introduced to control the snail vectors of bilharzia (Welcomme 1981). There have also been accidental transfers like that of *T. melanopleura*.

In all, about 50 fish species have been introduced to or transferred within Africa, but many of these did not establish themselves (FAO/CIFA 1985). Some of those which have done so have created important commercial fisheries: others have led to undesirable consequences. The most prominent effects of fishes introduced to Africa can be divided into three categories. The first includes species which have directly through predation and indirectly through competition depleted or even eliminated resident species. The second includes genetically and ecologically related species which have eliminated others through competition and/or hybridization. The third includes species that have caused or initiated environmental degradation.

Impacts of Predatory Species

Piscivores have often reduced or even eliminated many resident species in areas where they have been introduced. The Nile perch introduction into Lakes Victoria and Kyoga provides a spectacular example of the effects of introducing a large predator into a lake. As the population of the Nile perch in these lakes increased, many native species declined and some completely disappeared. Although the decline was initiated by human exploitation, predation by the Nile perch certainly contributed to the final elimination of many of the native species (Ogutu-Ohwayo 1990a).

As a juvenile, the Nile perch feeds on invertebrates and turns predominantly to fishes in the sub-adult and adult stages (Hamblyn 1966; Gee 1969; Okedi 1971; Ogutu-Ohwayo 1985; Ogari 1985). Soon after its introduction to Lakes Victoria and Kyoga, individuals of most sizes fed almost exclusively on haplochromine cichlids (Gee 1969; Okedi 1971; Ogutu-Ohwayo 1990b). Until establishment of the Nile perch, haplochromines were the most abundant fishes in these lakes and formed up to 80% by weight of the demersal fish stocks of Lake Victoria (Kudhongania and Cordone 1974; Okaronon et al. 1985). They were also as numerous in Lake Kyoga (Worthington 1929). After the establishment of the Nile perch halochromine stocks declined rapidly and are virtually absent in Lake Kyoga and extremely rare in many parts of Lake Victoria (Ogari 1985; Ogutu-Ohwayo 1985, 1990a, b). Even the larger species which had been reduced by human exploitation have been identified in Nile perch stomachs (Hamblyn 1966; Gee 1969) which confirms that the Nile perch contributed to their elimination.

Although never adequately exploited as a fishery, the Lake Victoria haplochromine species flock was one of the world's richest and included more than 300 endemic species (van Oijen et al. 1984). This diverse group of fishes had undergone much adaptive radiation and occupied many trophic levels. It contributed much to our understanding of the process of evolution by adaptive radiation and its decimation has been a great loss to evolutionary science.

Other predatory fishes, e.g., trout and bass have either depleted or eliminated other species in those waters to which they have been introduced. The black bass, *Macropterus salmoides*, introduced into Lake Naivasha in Kenya, depleted species which had earlier been introduced into the lake (Siddiqui 1977, Welcomme 1981). Similarly species of trout and large mouth bass, introduced into Southern Africa for sport and recreation, eliminated three native species (Jackson 1960, FAO/CIFA 1985).

Tilapiine Hybridization and Competition

Tilapiine species are known to form hybrids (Trewavas 1983) and introgressive hybridization may lead to genetic changes in the surviving species. Because many tilapiine species have similar ecological requirements, competition may lead to the elimination of one competitor. Both processes may happen concurrently making it difficult to ascertain their relative importance. In Africa, mixing of tilapiine species as a result of introductions appears to have resulted in elimination of some species through hybridization and/or competition. For instance, *Oreochromis spilurus* was introduced into Lake Naivasha (Kenya) in 1925 and became abundant during 1950's and 1960's (Siddiqui 1977). *Oreochromis leucostictus* was introduced in 1956 and hybridized with *O. spilurus*. This was followed by disappearance, first of *O. spilurus* then of the hybrids (Siddiqui 1977). In Lake Itasy (Madagascar), *O. macrochir* also disappeared after hybridizing with *O. niloticus* (Welcomme 1984). Moreau et al. (1988) identified several other incidences where hybridization of introduced *O. niloticus* with native tilapiines was suspected.

The disappearance of *Oreochromis esculentus* and *O. variabilis* which were endemic to Lakes Victoria and Kyoga could be due to hybridization and/or competition with introduced tilapiines especially *O. niloticus* and *T. zilli*. *T. zilli* may have competed with *O. variabilis* in the juvenile stages and affected its survival (Fryer 1961). Juvenile hybrids of *O. niloticus* and *O. variabilis* have been reported from Lake Victoria (Welcomme 1964; Trewavas 1983). Although no adult hybrids have been confirmed, adults have been found which combine the coloration of *O. variabilis* with the morphometry of *O. niloticus*. *Oreochromis niloticus* seems to be a superior competitor. It has a wider food spectrum, is more fecund, has a faster growth rate, has a longer life span and grows to a larger size than the endemic *Oreochromis* spp. (Fryer and Iles 1972). Because it cohabits with *L. niloticus* over much of its range *O. niloticus* may have evolved behavioral responses to reduce predation losses. Similar behavior by the native tilapiines in Lake Victoria would not have been necessary prior to the introduction of *L. niloticus*. Whereas the native *O. variabilitis* and *O. esculentus* were spatially segregated, *O. niloticus* occupies the habitats of both native species. This may have created competition for food and space.

In Lakes Victoria and Kyoga, it is difficult to separate the contributions of hybridization, competition, predation and

overfishing to the demise of the endemic *Oreochromis* species. Genetic analysis of the original *O. niloticus* stock from Lake Albert and the current *O. niloticus* populations in Lake Victoria and Kyoga might throw light on the putative role of hybridization. The other factors can only be evaluated through experimental and ecological studies if refugia for *O. esculentus* and *O. variabilis* can be found within Victoria or neighboring marginal lakes.

Ecosystem Alteration

Fish introductions can lead to ecosystem alterations which may select against native species. Compared with the direct effects of predation or competition, the effects of ecosystem alterations may be more subtle, but may have consequences for the entire fish community and total fish productivity rather than just for the immediate prey or competitor species. The common carp has often been introduced into ponds and small lakes in Africa where it increases turbidity by stirring up bottom sediments (Welcomme 1984; FAO/CIFA 1985). Hecky (1981) suggested that the trophic efficiency and water quality of the East African Great Lakes was at least in part the product of the distinctive fish faunas. Trophic cascade theory (Carpenter et al. 1985) has been invoked in Lake Michigan (Scavia et al. 1986) to account for increases in water clarity as the abundance of introduced piscivorous salmon peaked. According to this theory, increasing the abundance of fish at different trophic levels will have consequences for lower trophic levels. It predicts that increased piscivory should lead to reduced abundance of zooplanktivores, increased zooplankton abundance, reduced phytoplankton and increased water clarity through a cascade of interactions. A similar cascade of effects could be initiated by increasing the abundance of zooplanktivores (e.g., Turner 1982) leading to a reduction in herbivorous zooplankton abundance which would allow an increase in phytoplankton and a decrease in water clarity. At the base of the food chain, introduction of phytoplanktivores (e.g., Serruya et al. 1979) should lead to increased water clarity. The theory is important because it may explain changes in ecosystems as a consequence of fish introductions. African fish introductions offer an opportunity to test this theory in some of the largest lakes in the world where piscivores, zooplanktivores, and phytoplanktivores have been introduced both singly and in combination.

Significant ecosystem changes have been concurrent with or followed the introduction of, non-native fishes to Lakes Victoria and Kyoga. In Kyoga, the changes may be largely attributed to physical alterations unrelated to the introductions. At the time of the introductions to Kyoga, this 2700 km^2 lake had most of its surface covered by aquatic macrophytes; open water areas were restricted. High water levels in the early 1960's, combined with intense storms, sunk much of the vegetation and reduced the macrophytes to a fringing swamp. This shallow lake (maximum depth 4 m) now has extremely high phytoplankton biomass (20–40 $\mu g \cdot L^{-1}$ Chl *a*) and low Secchi disc transparency (<1 m). Because of the dramatic physical changes in Kyoga, it is difficult to isolate the effect of introductions from those due to habitat alterations. Nile perch catches are now falling from very high levels, but Nile Tilapia catches are rising (Ogutu-Ohwayo 1990b). High abundances of either the piscivore or the phytoplanktivore might be expected to depress phytoplankton abundance by the trophic cascade theory. In Lake Victoria, Secchi disc transparency has declined from values of 7–8 m recorded offshore by Worthington (1930) to 1.5–2.5 m currently. This change is a consequence of greatly increased phytoplankton crops (Ochumba and Kibara 1989; Hecky and Bugenyi 1991). These have been related to the increasing frequency of fish kills and the deoxygenation of the seasonal hypolimnion. Lake Victoria is exhibiting the classical symptoms of eutrophication. The cause would not follow directly from the successful introduction of the Nile perch and the Nile tilapia as the trophic cascade theory would predict that these changes by themselves would lead to lower phytoplankton densities. However, the disruption and reduction of the diverse and trophically complex haplochromine community by the introduced species may have initiated changes in food web structure and nutrient cycling which have led to a eutrophication response. Alternatively, changing land use may have increased nutrient loading and initiated an eutrophication response independent of the introductions. In any case Africa's largest lake (68 800 km^2) has been dramatically altered, raising concern about its long term productivity and certainly requiring greater understanding to effect its proper management.

The introductions of *Limnothrissa miodon* to Kivu and Kariba have not been accompanied by any known detrimental effects to the fish community structure or ecosystem function. De Iongh et al. (1983) found the zooplankton community and Secchi disc transparency of Kivu essentially unchanged (cf. Verbeke 1957) two decades after the introduction. However, Dumont (1986), based on only a few zooplankton collections, has expressed concern that *Limnothrissa* has decimated its zooplankton resource in Lake Kivu. In Kariba the clupeid fishery expanded rapidly as effort increased, but Marshall (1988) now suggests that the yield is determined by nutrient supply. Green (1985) concluded that *Limnothrissa* had reduced zooplankton abundance in Kariba by 2.4 to 44 times depending on the taxon approximately one decade after the clupeid had become abundant. The introduction of *Limnothrissa* into Kivu and Kariba without apparent affect on other fish species probably reflects the simple fish faunas which occurred naturally in those lakes. Kariba is a man-made lake whose original fauna was derived from riverine species, none of which successfully exploited the pelagic region of this huge reservoir, while Kivu had an extremely impoverished fauna as the result of catastrophic fish kills related to volcanic activity (Haberyan and Hecky 1987) in its recent history. Given the dramatic alteration of the complex, endemic fauna and the ecosystem properties of Victoria following the introduction of non-native species, the cautions of McKay et al. (1985) and Eccles (1985) concerning the introduction of the clupeids of Lake Tanganyika into Malawi and other lakes with more complex faunas are well founded. The clupeid fishery is a seductive development option to increase fish yields, but our present limited understanding of the ecology of the native fish communities precludes prediction of the consequences of an introduction some of which may be highly undesirable.

Economic Implications of Fish Introduction

Despite the ecological and genetic outcomes of fish introductions, increases in production have been of much benefit to people in various parts of Africa. Most African countries are poor, and alternative sources of animal protein, such as beef and poultry, are not well developed and can be afforded only by the rich few. Malnutrition is a concern in many African countries. In the vicinity of lakes and rivers, people depend on fish as their cheapest source of animal protein.

The Nile perch and the Nile tilapia which were introduced in Lakes Victoria and Kyoga have so far resulted in tremendous increases in the quantities of fish landed (Ogutu-Ohwayo 1990a, b). In Lake Kyoga, the quantity of fish landed increased over ten fold from an annual catch of about 4 500 tons at the time of introduction of new fishes in 1956 to a record of 160 000 tons in 1977 to which the introduced species contributed about 80%. In Lake Victoria, the total quantity of fish landed from the Ugandan, Kenyan and Tanzanian parts of the lake has increased between two and six fold following establishment of the Nile perch and the Nile tilapia. In the Ugandan part of the lake, commercial catches increased from 17 000 tons in 1983 to 132 000 tons in 1989, in the Kenyan part from 20 000 tons in 1977 to 123 000 tons in 1988 and in the Tanzanian part from 64 000 in 1982 to 89 600 tons in 1985 following establishment of the introduced species. *Limnothrissa miodon*, a clupeid endemic to Lake Tanganyika, which was successfully introduced into Lake Kariba, increased catches from less than 1 000 in 1974 to about 24 000 tons by 1985 (Marshall 1988) and is now the most important fishery in Lake Kariba. The clupeid also migrated down the Zambezi River into Cabora Bassa Reservoir where it may provide a potential yield of 8 000 tons (Petr and Kapetsky 1983). Its introduction to Lake Kivu has also created a significant pelagic fishery there.

However, introductions may only have short term benefits and more understanding is needed for their utilization as a tool in fisheries management. This can be seen from the many unsuccessful introductions that have been made and the successful ones that have not sustained production. It is not yet clear whether the fisheries of Lakes Victoria and Kyoga will stabilize and for how long high catches will be sustained. Catches of Nile perch in Lake Kyoga, where it was introduced and became established earlier than in Lake Victoria, have declined after dominating the fishery during the 1960's and 1970's (Ogutu-Ohwayo 1990b). Similar changes are expected in Lake Victoria once the haplochromine prey are depleted.

Conclusions

Introduction of new fish species have contributed to increased yields in many African lakes where fish is an important source of protein. Unfortunately, this has sometimes been accompanied by undesirable consequences which have varied from displacement to total destruction of the resident fish populations, loss of genetic identity, and environmental degradation. This emphasizes the need to have guidelines on fish introductions and regulations to prohibit unauthorized release of non-native fishes. Such guidelines have been lacking in Africa, but the Committee for the Inland Fisheries of Africa of the FAO are now initiating guidelines on introduction or transfer of fishes there. Special consideration must be given to the complex and diverse species flocks in the African Great Lakes.

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Fish Introductions in Europe with Particular Reference to its Central and Eastern Part[1]

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Holčík, J. 1991. Fish introductions in Europe with particular reference to its central and eastern part. Can. J. Fish. Aquat. Sci. 48 (Suppl. 1): 13–23.

At least 134 exotic and/or translocated fish species belonging to 34 families which were introduced to 29 of 33 European countries are documented. These include 35 species of Cyprinidae (introduced to 28 countries), 17 Salmonidae (28), 11 Coregonidae (12), 10 Cichlidae (8), six Centrarchidae (23), five Acipenseridae (8), four Ictaluridae (18), four Poeciliidae (11), four Percidae (9), four Mugilidae (1), three Catostomidae (6), three Gasterosteidae (5), two Anguillidae (3), two Atherinidae (2), two Clariidae (4), two Gobiidae (2), two Umbridae (6), two Pleuronectidae (1), two Thymallidae (3) and one species each of Anabantidae (1), Channidae (2), Clupeidae (1), Cobitidae 91), Eleotridae (1), Engraulidae (1), Esocidae (3), Mullidae (1), Osmeridae (1), Percichthyidae (1), Petromyzontidae (1), Polyodontidae (2), Siluridae (5), and Syngnathidae (1). True exotic species amount to 74 species/forms belonging to 21 families, of which 11 families are exotic for Europe. The remaining 60 species (21 families), are native in Europe and were translocated among various watersheds and/or countries. Most species were intentionally released since 1945 to enhance sport, commercial and subsistence fisheries, for fish farming and aquaculture, and for purposes such as mosquito, macrophytes and algal bloom control. Poor success was registered in most cases, along with adverse or unexpected effects on native fishes and their habitat.

Le présent article documente l'introduction dans 29 pays européens sur 33 d'au moins 134 espèces de poissons exotiques ou transplantées appartenant à 34 familles différentes, soit 35 espèces de Cyprinidae (introduites dans 28 pays), 17 Salmonidae (28), 11 Coregonidae (12), 10 Cichlidae (8), 6 Centrarchidae (23), 5 Acipenseridae (8), 4 Ictaluridae (18), 4 Poeciliidae (11), 4 Percidae (9), 4 Mugilidae (1), 3 Catostomidae (6), 3 Gasterosteidae (5), 2 Anguillidae (3), 2 Atherinidae (2), 2 Clariidae (4), 2 Gobiidae (2), 2 Umbridae (6), 2 Pleuronectidae (1) 2 Thymallidae (3) et une espèce de chacune des familles suivantes : Anabantidae (1), Channidae (2), Clupeidae (1), Cobitidae (1), Eleotridae (1), Engraulidae (1), Esocidae (3), Mullidae (1), Osmeridae (1), Percichthyidae (1), Petromyzontidae (1), Polyodontidae (2), Siluridae (5), et Syngnathidae (1). On compte 74 espèces ou formes vraiment exotiques appartenant à 21 familles, parmi lesquelles 11 sont exotiques (pour l'Europe). Les 60 autres espèces (21 familles) sont indigènes et ont été transplantées dans des bassins hydrographiques ou des pays différents. Depuis 1945, la plupart des espèces ont été libérées intentionnellement dans le but d'améliorer les pêches sportive, commerciale et de subsistance, pour les besoins de la pisciculture et de l'Aquiculture et pour d'autres raisons, comme la lutte contre les moustiques, les macrophytes et les proliférations d'algues. Outre le peu de succès obtenu dans la plupart des cas, on a observé des effets néfastes ou imprévus sur les poissons indigènes et leur habitat.

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Introductions and/or translocation of fish in Europe may be traced back to the beginning of first century A.D., when some species of fish, mostly marine, but also freshwater, were held in *piscinae* by the Romans (Balon 1969). The common carp, *Cyprinus carpio*, seems to have been the first freshwater species transferred from its native range, first to Rome and then to other countries in Europe (Balon 1974). With expanding Christianity, the construction of ponds became a necessity and nearly all the more important monasteries or parishes kept fish transferred from neighbouring streams. Later, the nobility also followed this custom and during the Renaissance fish farming became a widespread fashion throughout Europe. The idea of transferring fish from other continents probably also arose during Renaissance times. However, large-scale introductions of fish species into areas outside of their native range is a comparatively recent phenomenon and the majority of fish translocations date from the second half of the last century.

Recently, Welcomme (1981, 1988) compiled lists of international transfers of inland fish species and provided an analysis of trends, motives, risks and evaluation of introductions, globally. In this review, I wish to describe the situation in Europe, especially in Central and Eastern Europe, which was not so thoroughly covered by Welcomme. Because of limited space, I wish to give only a general account of this subject and the more detailed analysis will be published later.

Definitions

Definitions used in this paper follow those by Karpevich (1975), and Shafland and Lewis (1984). *Introduced* species

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include any species intentionally or accidentally transported and released by man into an environment outside its original area. *Exotic* is a species not native to a given watershed, but, in this review, I am distinguishing the *true exotic* and the *translocated* species. The latter term has an exclusively political aspect to designate a species which is exotic for a given country or for some watershed inside it, but not in Europe, while the term exotic *sensu stricto*, is used here only for species not native within the mainland and insular Europe. *Acclimatization* is a process of adaptation of an introduced species and their offspring in the new environment. The final phase of acclimatization is *naturalization*, when the introduced species finds a "vacant niche" in a community, which means that it adapts to food, space, spawning grounds, etc., which are not fully exploited by native species in a given water body (Nilsson 1984).

In this paper, the subcontinent of Europe is considered by its generally accepted boundaries: it is separated from Asia by the Ural Mountains, Ural River, and Caspian Sea on the east, and by the depression of the Manych River, Caucasus Mountains, Sea of Azov, the Strait of Kerch, Black Sea, Bosporus, Sea of Marmara, Dardanelles, and the Aegean Sea on the south east. The Caucasus Mountains are excluded from Europe in this definition although included by all Soviet geographers. The island of Cyprus is considered to be a European country in this paper. Turkey is not mentioned as no data exist on its fish introductions and Germany is considered as one country within its present boundaries.

Because of limited space on the one hand and the enormous literature on the other, only a selected list of the most important items is introduced in the list of references. This list is predominantly restricted to the recent monographs dealing with fishes in particular European countries, special reports, compendia and also synthetic papers dealing with fish introductions in Europe. English translations of their titles are added in those cases where the paper under consideration was published in a language other than English, French, German, Spanish or Italian.

The following symbols and/or evaluation of the introduced species are used in Tables 1 and 2:

A = species used in aquaculture with artificial reproduction only. If another symbol is used in conjunction with A it means that species is used and reproduced predominantly in aquaculture;
D = species disappeared;
E = species established in nature in more than 50% of countries;
R = species rare, occurring in nature in less than 50% of countries;
* denotes family exotic for Europe.

Countries are arranged alphabetically and those which introduced particular species first in Europe are printed in italics. The year of first introduction to Europe of a species is also indicated along with the country to which it was first introduced.

Number of Species and Receiving Countries

All species of fish and lampreys known to be the subject of acclimatization experiments in Europe have been summarized (Tables 1 and 2). A total of 134 species were recorded belonging to 34 families, of which 11 are exotic for Europe (Table 3). There are 74 true exotic species belonging to 21 families, while there are 60 translocated species belonging to 21 families.

The most frequent introductions involved cyprinids followed by salmonids and coregonids. These three families include 63 species (30 exotic and 33 native) and share slightly more than 47% of the total number of both exotic and translocated species.

As may be expected, the first introductions were translocations of some native European species among various watersheds and/or countries. As already mentioned, it was the common carp that was introduced step by step southward, westward and also northward from its native river basin, the Danube. This process began very early, most probably between first and fourth century A.D. (Balon 1974) and proceeded very rapidly, as the medieval annals indicate that between the seventh and twelfth centuries mass culturing of this species existed almost throughout Europe (Brylińska et al. 1986). Together with carp, other species certainly were also transferred, among them the crucian carp (*Carassius carassius*) and another cyprinid, *Leucaspius delineatus*, the natural distribution of which was probably limited by the Rhine (Berg 1949). Attempted intentional introductions of other species probably dated back as for as those of carp, however, there are no data on these, possibly because the lower hardiness of these species caused their introductions to fail. Among the few exceptions to this is the medieval introductions of the northern pike (*Esox lucius*) to Ireland (Fitzmaurice 1984) in the thirteenth to fourteenth century as indicated by Welcomme (1988) and also several attempts to introduce the sterlet (*Acipenser ruthenus*) into the Baltic Sea, White Sea, and even the Barents Sea watersheds during the middle of the eighteenth century (Linnaeus 1758; Mohr 1952; Burmakin 1963; Witkowski 1989).

The first attempts to introduce true exotic fish species are not exactly known, but they are certainly older than those performed in the second half of the nineteenth century, when the modern era of introductions began. These introductions all involved North American species, the salmonids, followed by catfishes and centrarchids and also one coregonid species. The first was the brook trout (*Salvelinus fontinalis*) introduced to the United Kingdom in 1869, followed by the chinook salmon (*Oncorhynchus tschawytscha*), the rainbow trout (*Oncorhynchus mykiss*, syn. *Salmo gairdneri*) and the lake trout (*Savelinus namaycush*) subsequently imported by France and the Netherlands, Germany (Poland), and by Germany and Switzerland, respectively. Two easily confused American catfishes, the black bullhead (*Ictalurus melas*) and the brown bullhead (*I. nebulosus*) and six centrarchids (*Ambloplites rupestris, Lepomis cyanella, L. gibbosa, L. aurita, Micropterus dolomieui, M. salmoides*) were also introduced, mostly to Western Europe, up until the end of the nineteenth century.

Since the beginning of the twentieth century, the rate of introductions has increased rapidly. There is, however, some difference between the relative rate of introductions of the native and the true exotic species. By the end of the second World War, the percentage of the native fish introductions was 66.7%, which has since decreased by half to 33.3%. In the case of the introductions of the true exotic species the trend is exactly the opposite, in that the number of species introduced since 1945 has doubled and the initial (pre 1945) rate of 31.0% has increased to 69.0%.

There are records on introductions for 29 of the 33 European countries. Only Andorra, Monaco, San Marino and Vatican are not listed among countries receiving fish species from outside. This does not mean that they did not introduce fish species in the past, but rather that there are no available records for them. It may be that data for these little countries are included in

TABLE 1. A list of exotic fishes introduced in Europe (including diffusion between countries). For explanation see text.

Species	Year of first introduction	Status	Country
ACIPENSERIDAE			
Acipenser baeri Brandt, 1869	1956	A	France, Hungary, *USSR*
Acipenser fulvescens Rafinesque, 1817	1969	A	USSR
Acipenser transmontenus Richardson, 1836	1987	A	Italy
*POLYODONTIDAE			
Polyodon spathula (Walbaum, 1792)	1974	A	Hungary, *USSR*
ANGUILLIDAE			
Anguilla australis schmidti Phillips, 1925	1975	D	Italy
Anguilla japonica Temminck et Schlegel, 1842	?	A	France, Germany, Italy
CYPRINIDAE			
Aristichthys nobilis Richardson, 1836	1954	A, R	Albania, Austria, Bulgaria, Czecho-Slovakia, France, Germany, Hungary, Italy, Netherlands, Poland, Romania, *USSR*, Yugoslavia
Barbus schwanenfeldi Bleeker, 1853	?	D	Italy
Capoeta capoeta sevangi Filippi, 1865	1950s	D	USSR
Catla catla (Hamilton-Buchanan, 1822)	1966	A	USSR
Cirrhinus mrigala (Hamilton-Buchanan, 1822)	1966	A	USSR
Ctenopharyngodon idella (Cuvier et Valenciennes, 1844)	1949	A, R	Albania, Austria, Belgium, Bulgaria, Cyprus, Czecho-Slovakia, Denmark, France, Germany, Greece, Hungary, Italy, Netherlands, Poland, Romania, Sweden, UK, *USSR*, Yugoslavia
Cyprinus carpio haematopterus Temminck et Schlegel, 1842	1947	A, R	Czecho-Slovakia, *USSR*
Hypophthalmichthys molitrix (Valenciennes, 1844)	1953	A, R	Albania, Austria, Belgium, Bulgaria, Cyprus, Czecho-Slovakia, Denmark, France, Germany, Greece, Hungary, Italy, Netherlands, Poland, Romania, Sweden, UK, *USSR*, Yugoslavia
Labeo rohita (Hamilton-Buchanan, 1822)	1966	A	USSR
Megalobrama terminalis (Richardson, 1845)	1963	D	Albania, *Hungary*, Yugoslavia
Mylopharyngodon piceus (Richardson, 1845)	1963	A	Albania, Czecho-Slovakia, Germany, *Hungary*, Romania, USSR
Parabramis pekinensis (Basilewski, 1855)	1963	D	Hungary
Pimephales promelas Rafinesque, 1820	1983	E	*Belgium*, France, Germany
Pseudorasbora parva (Schlegel, 1842)	1960	E	Albania, Austria, Bulgaria, Czecho-Slovakia, Germany, Hungary, *Romania*, USSR, Yugoslavia
*CATOSTOMIDAE			
Ictiobus bubalus (Rafinesque, 1812)	1971	A	Romania, *USSR*
Ictiobus cyprinella (Cuvier et Valenciennes, 1844)	1971	A	Czecho-Slovakia, Bulgaria, Hungary, Romania, *USSR*
Ictiobus niger (Rafinesque, 1819)	1971	A	Bulgaria, Czecho-Slovakia, Hungary, Poland, Romania, *USSR*
*ICTALURIDAE			
Ictalurus melas (Rafinesque, 1820)	1871	E	Belgium, *France*, Hungary, Ireland (?), Italy, Netherlands, Norway, Switzerland, Spain, UK
Ictalurus natalis (LeSueur, 1819)	1906	E	Italy
Ictalurus nebulosus (LeSueur, 1819)	1885	E	Austria, Czecho-Slovakia, Finland, France, *Germany*, Hungary, Ireland (?), Italy, Netherlands, Poland, Romania, Spain, UK, USSR, Yugoslavia
Ictalurus punctatus (Rafinesque, 1818)	1968	A, R	Belgium, Cyprus, Czecho-Slovakia, France, Hungary, Italy, *UK*, USSR, Yugoslavia
*CLARIIDAE			
Clarias batrachus (Linnaeus, 1758)	?	R	UK
Clarias lazera (Valenciennes, 1840) (syn. *Clarias gariepinus* (Burchell, 1842))	1974	A	*Cyprus*, Czecho-Slovakia, Netherlands
UMBRIDAE			
Umbra pygmaea DeKay, 1842	1913	R	Belgium, *France*, Germany, Netherlands
COREGONIDAE			
Coregonus autumnalis migratorius (Georgi, 1775)	1949	D	USSR
Coregonus clupeaformis (Mitchill, 1818)	1881	D	*France*, *Germany*, Italy (?), Netherlands, Switzerland, UK
Coregonus lavaretus baunti Mukhomedyarov, 1948	1953	D	USSR

TABLE 1. (*Continued*)

Species	Year of first introduction	Status	Country
Stenodus leucichthys nelma (Pallas, 1773)	1953	D	USSR
THYMALLIDAE			
Thymallus baicalensis Dybowski, 1874	1959	D	*Czecho-Slovakia*, Poland
SALMONIDAE			
Oncorhynchus clarki (Richardson, 1836) (syn. *Salmo clarki*)	1960s	A,R	Cyprus, Denmark, Sweden
Oncorhynchus gorbuscha (Walbaum, 1792)	1939	D,R	Finland, Ireland, Norway, Poland, UK, *USSR*
Oncorhynchus keta (Walbaum, 1792)	1932	D	Finland, *USSR*
Oncorhynchus kisutch (Walbaum, 1792)	1971	D	Cyprus, *France,* Germany, Greece, Italy, Netherlands, Spain, Yugoslavia
Oncorhynchus mykiss (Walbaum, 1792) (syn. *Salmo gairdneri* (Richardson, 1836)	1882	A, R	Albania, Austria, Belgium, Bulgaria, Cyprus, Czecho-Slovakia, Denmark, Finland, *France, Germany,* Greece, Hungary, Iceland, Ireland, Italy, Liechtenstein, Luxemburg, Netherlands, Norway, Poland, Portugal, Romania, Spain, Sweden,Switzerland, UK, USSR, Yugoslavia
Oncorhynchus nerka (Walbaum, 1792)	1959	D	Denmark, Finland, *Sweden*
Oncorhynchus rhodurus (Jordan et McGregor, 1925)	1976	D	Germany
Oncorhynchus tschawytscha (Walbaum, 1792)	1877	D	Denmark, Finland, *France,* Germany, Ireland, Italy, *Netherlands,* UK
Salmo ischchan Kessler, 1877	1949	D	USSR
Salvelinus fontinalis Mitchill, 1815	1869	R, A	Austria, Belgium, Bulgaria, Cyprus, Czecho-Slovakia, Denmark, Finland, France, Germany, Greece, Hungary, Italy, Netherlands, Norway, Poland, Romania, Spain, Sweden, Switzerland, *UK,* USSR, Yugoslavia
Salvelinus leucomaenis pluvius (Hilgendorf, 1876)	1977	A, (D?)	Germany
Salvelinus namaycush (Walbaum, 1792)	1888	R	Czecho-Slovakia, Denmark, Finland, France, Italy, *Germany,* Spain, Sweden, *Switzerland,* UK
*POECILIIDAE			
Gambusia affinis (Baird et Girard, 1853)	1921	E	France, Greece, Hungary, Italy, *Portugal,* Romania, *Spain,* USSR, Yugoslavia
Poecilia reticulata (Peters, 1859)	1963	R	Czecho-Slovakia, Hungary, Italy, Netherlands, UK
Poecilia sphenops Valenciennes, 1846	?	R	Czecho-Slovakia, Hungary
Xiphophorus helleri Heckel, 1848	?	R	Czecho-Slovakia, Hungary
ATHERINIDAE			
Odontesthes bonariensis (Valenciennes, 1853)	1970	R	Italy
*PERCICHTHYIDAE			
Morone saxatilis (Walbaum, 1792)	1965	D	USSR
*CENTRARCHIDAE			
Ambloplites rupestris (Rafinesque, 1817)	1930	E	France, *UK*
Lepomis aurita (Linnaeus, 1758)	1895	E	*Germany*, Italy
Lepomis cyanella Rafinesque, 1819	?	R	Germany
Lepomis gibbosa (Linnaeus, 1758)	1885	E	Austria, Belgium, Bulgaria, Czecho-Slovakia, *France,* Germany, Greece, Hungary, Italy, Netherlands, Poland, Portugal, Romania, Spain, Switzerland, USSR, Yugoslavia
Micropterus dolomieui Lacépède, 1802	1873	R	Austria, Belgium, Czecho-Slovakia, Denmark, *Finland*, France, Germany, Norway, Sweden, UK
Micropterus salmoides (Lacépède, 1802)	1877	R, A	Belgium, Cyprus, Czecho-Slovakia, Denmark, Finland, *France*, Germany, Hungary, Italy, Netherlands, Poland, Portugal, Spain, UK, USSR, Yugoslavia
PERCIDAE			
Stizostedion vitreum (Mitchill, 1818)	1925	D	UK
*CICHLIDAE			
Astronotus ocellatus (Cuvier, 1829)	?	D	Italy
Cichlasoma facetum (Jenyns, 1842)	1940s	R	Portugal
Oreochromis aureus (Steindachner, 1864)	1976	A	*Cyprus,* Czecho-Slovakia, USSR
Oreochromis mossambicus (Peters, 1852)	1962	A, R	Czecho-Slovakia, Malta, UK, *USSR*
Oreochromis niloticus (Linnaeus, 1758)	1957	A	Belgium, Cyprus, Czecho-Slovakia, *Germany*
Oreochromis urolepis hornorum (Trewavas, 1966)	?	A	Czecho-Slovakia, *USSR*

TABLE 1. (*Concluded*)

Species	Year of first introduction	Status	Country
Sarotherodon melanotheron Rüppell, 1852	?	A	USSR
Tilapia guineensis (Bleeker, 1863)	?	A	USSR
Tilapia mariae (Boulenger, 1899)	?	A	USSR
Tilapia zillii (Gervais, 1853)	1925	A, R	*UK*, USSR
MUGILIDAE			
Mugil soiuy Basilewski, 1855	1972	R	USSR
*ELEOTRIDAE			
Perccottus glehni Dybowski, 1877	1950s	E	USSR
*ANABANTIDAE			
Osphronemus goramy Lacépède, 1802	?	D (?)	Italy
*CHANNIDAE			
Channa argus warpachowskii Berg, 1909	1949	R	Czecho-Slovakia, *USSR*

references dealing with their larger neighbours, Spain, France and Italy, respectively. The frequency of introductions of particular species varies considerably. Although the most popular candidates for introductions come from families Salmonidae, Cyprinidae, Centrarchidae, Ictaluridae and Coregonidae, which were imported to and/or translocated in 28, 28, 23, 18, and 12 countries, respectively, the majority of species have only been introduced to a few countries. While there seems to be some correlation between the size of the country and the number of species introduced (Table 4), there are also exceptions showing for instance, that Hungary which is far smaller than Norway (93 032 km^2 versus 323 920 km^2) introduced four times as many fish species (28 versus 7). As expected, the Soviet Union also plays the role of the super power in this respect, as it introduced to, and transferred on its European territory 70 species including 40 exotic and 30 native, i.e. slightly more than half of the total number of fish species received by all other European countries.

Motives for Introduction

There are significant differences concerning the motives for the introductions between the true exotic and the native European species. In the first case, the rank of motives is as follows: aquaculture, including experimental (30.6%), accident (21.0), unknown reasons (15.5), improvement of the wild stock[3] (14.7), sport (9.1), biomanipulation[4] (7.1) and ornament (2.0). In the second group, translocated species, the primary motive for introduction was the improvement of the wild stock (37.6%), followed by unknown reasons (20.8), accident (18.4), sport (12.0), aquaculture (7.2) and ornament (4.0). The motives for introductions vary from country to country. In the USSR, for instance, most species, both exotic and native, were introduced or translocated to improve the wild stock and aquaculture is secondary, while in other countries aquaculture predominates followed then by sport. There are also considerable differences in the approach of some countries to the same species. The brown bullhead, for instance, was introduced for aquaculture by Yugoslavia, Poland and Germany, but for the improvement of the wild stock by Finland and the USSR.

Evaluation of Introductions

Almost all introductions into natural ecosystems made prior to the second World War may be considered to a certain degree as a gamble. The situation improved after the war, as greater awareness of ecology developed and introduction experiments started to be planned on a scientific basis. Here the leading role has been played by the Soviet Union, where the theory and practice of introductions and acclimatization of fish is based on ecological principles (Zenkevich 1940; Dryagin 1954; Burmakin 1961,1963; Karpevich 1965a, b, 1975; Rass 1965). At the present time, almost all intentional introductions are more or less carefully planned. According to Burmakin (1963) up until 1957, 1 398 water bodies in the USSR (of which 87% were lakes, 7% reservoirs and 6% rivers) were planted with 51 species of freshwater fish belonging to 12 families. However, naturalization of both exotic and translocated species was only attained in 12% of these water bodies. Furthermore, catches of acclimated fish lagged considerably behind the effort exerted for their introductions. From the data presented by Karpevich et al. (1975) and Burmakin and Shimanovskaya (1975), one can calculate that between the periods 1957/1963 and 1964/1971 the mean annual number of plantings of exotic fishes rose by 123%, the number of water bodies stocked by 164% and the quantity of fishes (including the eggs, juveniles and adults) introduced by 229%. However, the catch of introduced fishes in the same period increased only by 56% and its percentage share to the total inland fish catch (the most part of which is probably shared by fish from aquaculture) only by 61%. According to the last evaluation of Lifshits and Belousov (1979) only 3% of all introductions released in the USSR up until 1978 gave a commercial benefit. The discrepancy between the effort and result of introduction is explained mainly by the lack of biological justification, insufficient analysis and generalization of experience obtained, by the slow development of the theory of acclimatization and by shortcomings in the actual practice and organization of the introductions (Karpevich et al. 1975; Lifshits and Belousov 1979).

There are, however, some examples of successful introductions. Three species of mullets (Mugilidae), viz. *Liza aurata, L. saliens* and *Mugil cephalus*, which were transferred from the

[3]This term is rather vague and in some European countries, like in Czecho-Slovakia, for instance, the term "enrichment of the native fish fauna" is used. According to Welcomme (1988) this term includes establishing new food fisheries, filling a "vacant niche," stocking natural waters, providing forage for predators, restoration of fisheries, establishing a wild stock and the control of stunted species.

[4]Including mosquito, macrophytes, algal blooms and forage fish species control.

TABLE 2. A list of translocated fishes within the Europe (including diffusion between countries).

Species	Year of first introduction	Status	Country
PETROMYZONTIDAE			
Caspiomyzon wagneri (Kessler, 1870)	1968	D	USSR
ACIPENSERIDAE			
Acipenser gueldenstaedti Brandt, 1833	1962	D	Finland, Sweden, *USSR*
Acipenser ruthenus Linnaeus, 1758	1763	R	Finland, France, Germany, Poland, Sweden, *USSR*
CLUPEIDAE			
Clupeonella cultriventris (Nordmann, 1840)	?	E	USSR
ENGRAULIDAE			
Engraulis encrasicholus (Linnaeus, 1758)	1931	D	USSR
CYPRINIDAE			
Abramis ballerus (Linnaeus, 1758)	1957	E	USSR
Abramis bjoerkna (Linnaeus, 1758)	?	R	Cyprus, Italy
Abramis brama (Linnaeus, 1758)	1932	R	Italy, Spain, *USSR*
Alburnus alburnus (Linnaeus, 1758)	?	E	Cyprus, Spain
Aspius aspius (Linnaeus, 1758)	1984	D	Netherlands
Barbus barbus (Linnaeus, 1758)	1956	E	UK
Carassius auratus (Linnaeus, 1758)	?	E	Albania, Austria, Bulgaria, Cyprus, Czecho-Slovakia, Germany, Hungary, Italy, Poland, Portugal, Spain, UK, USSR, Yugoslavia
Carassius carassius (Linnaeus, 1758)	?	E	Belgium, Cyprus, France
Cyprinus carpio Linnaeus, 1758	?	E, A	Albania, Belgium, Cyprus, Czecho- Slovakia, Denmark, Finland, France, Germany, Greece, Ireland, Italy, Liechtenstein, Luxemburg, Malta, Netherlands, Norway, Poland, Portugal, Spain, Sweden, Switzerland, UK, USSR
Gobio gobio (Linnaeus, 1758)	1899	E	*Portugal*, Spain
Leucaspius delineatus (Heckel, 1834)	?	E	Belgium
Leuciscus idus (Linnaeus, 1758)	1874	R	Netherlands, Spain, *UK*
Leuciscus leuciscus (Linnaeus, 1758)	1889	E	Ireland
Leuciscus souffia Risso, 1826	?	D	Spain
Pelecus cultratus (Linnaeus, 1758)	1957	E	USSR
Rhodeus sericeus (Pallas, 1776)	1920s	R	UK
Rutilus frisii kutum (Kamenskii, 1891)	1933	D	USSR
Rutilus rutilus (Linnaeus, 1758)	1889	E	Cyprus, *Ireland*
Scardinius erythrophthalmus (Linnaeus, 1758)	?	R	Spain
Tinca tinca (Linnaeus, 1758)	1600s	E	Finland, *Ireland*, Norway
Vimba vimba (Linnaeus, 1758)	1957	D	USSR
COBITIDAE			
Misgurnus fossilis (Linnaeus, 1758)	?	E	Spain
SILURIDAE			
Silurus glanis (Linnaeus, 1758)	1881	R	Belgium, Cyprus, *Denmark*, Italy, Spain
ESOCIDAE			
Esox lucius (Linnaeus, 1758)	1200s	E	*Ireland*, Portugal, Spain
UMBRIDAE			
Umbra krameri Walbaum, 1792	1925	R	Poland, *UK*
OSMERIDAE			
Osmerus eperlanus (Linnaeus, 1758)	1932	E	USSR
COREGONIDAE			
Coregonus albula (Linnaeus, 1758)	1872	R (D)	Czecho-Slovakia, Hungary, Romania, *USSR*
Coregonus autumnalis autumnalis (Pallas, 1776)	1960	D	Czecho-Slovakia
Coregonus lavaretus (Linnaeus, 1758) *s. lato*	1861	R, A	Belgium, Czecho-Slovakia, Germany, Greece, Hungary, *Italy*, Netherlands, Romania, USSR, Yugoslavia
Coregonus muksun (Pallas, 1814)	1984	D	Poland
Coregonus nasus (Pallas, 1776)	?	R	Belgium, USSR
Coregonus peled Gmelin, 1789	1954	E, A	Czecho-Slovakia, Finland, Germany, Hungary, Poland, *USSR*, Yugoslavia
Stenodus leucichthys leucichthys (Guldenstadt, 1772)	1925	D	USSR
THYMALLIDAE			
Thymallus thymallus (Linnaeus, 1758)	?	R	Italy

TABLE 2. (*Concluded*)

Species	Year of first introduction	Status	Country
SALMONIDAE			
Hucho hucho hucho (Linnaeus, 1758)	1888	R, (D)	Belgium, *Czecho-Slovakia*, France, Poland, Spain, Sweden, Switzerland, UK
Salmo salar Linnaeus, 1758	1866	D	Cyprus, Greece, *Italy*, USSR
Salmo trutta Linnaeus, 1758	1970	R	Cyprus
Salvelinus alpinus (Linnaeus, 1758)	1955	R, (D, A)	Cyprus, *Denmark*, France, Ireland, Italy, Netherlands, Spain, Yugoslavia
Salvelinus salvelinus (Linnaeus, 1758)	1851	R	*Czecho-Slovakia*, France, Yugoslavia
ATHERINIDAE			
Atherina mochon pontica Eichwald, 1831	?	E	USSR
GASTEROSTEIDAE			
Gasterosteus aculeatus Linnaeus, 1758	?	E	Austria, Czecho-Slovakia, Hungary, Italy
Pungitius platygaster (Kessler, 1859)	1981	R	USSR
Pungitius pungitius (Linnaeus, 1758)	?	R	Austria
SYNGNATHIDAE			
Syngnathus nigrolineatus Eichwald, 1831	?	E	USSR
PERCIDAE			
Gymnocephalus cernuus (Linnaeus, 1758)	1982	E	UK
Perca fluviatilis Linnaeus, 1758	1971	E	Cyprus
Stizostedion lucioperca (Linnaeus, 1758)	?	E	Czecho-Slovakia, Denmark, France, Germany, Italy, Netherlands, UK, USSR
MULLIDAE			
Mullus barbatus ponticus Essipov, 1927	1931	D	USSR
MUGILIDAE			
Liza aurata (Risso, 1810)	1930	E	USSR
Liza saliens (Riso, 1810)	1930	E	USSR
Mugil cephalus Linnaeus, 1758	1930	E	USSR
GOBIIDAE			
Neogobius fluviatilis (Pallas, 1811)	1970	E	Hungary
Neogobius melanostomus (Pallas, 1811)	?	E	USSR
PLEURONECTIDAE			
Platichthys flesus luscus (Pallas, 1811)	1902	D	USSR
Scophthalmus maeoticus (Pallas, 1811)	1930	D	USSR

Black Sea to the Caspian Sea in 1930, fully acclimated and naturalized there and now constitute commercially important species, not only in the USSR, but also in Iran. Attempts to introduce the peled whitefish (*Coregonus peled*) were also successful in lakes, impoundments and for aquaculture in the European part of the USSR, and in Czecho-Slovakia, Poland and Germany. These are, however, rather the exceptions and most attempts to establish some exotic species in nature have failed. Thus, the naturalization of the grass carp (*Ctenopharyngodon idella*) and the silver carp (*Hypophthalmichthys molitrix*) was successful only in two rivers in the European USSR, the Kuban' and the Volga (Motenkov 1966; Kazancheev 1981), in the Terek River flowing from Caucasus Mountains (Abdusamadov 1986), and, probably also in the Tisza River in Hungary (Tóth and Biró 1984), although many attempts were made to acclimatize them, especially in the USSR. The release of coregonids into reservoirs of the USSR has not been successful (Berka 1990) and the members of this family naturalized only as rare exceptions. Moreover, several introductions of the Pacific salmons such as *Oncorhynchus keta* and *O. gorbuscha* in the Barents Sea and even in the Caspian Sea made by the USSR since early 30's, almost completely failed, as well as did earlier experiments with *O. kisutch, O. nerka* and *O. tschawytscha* conducted by Western European countries including the United Kingdom, France, Denmark, Italy, Sweden, Germany and Yugoslavia.

Of three species of sturgeons, *Acipenser ruthenus, A. baeri,* and *A. gueldenstaedti*, introduced mainly by the USSR into the Baltic Sea watershed, none became established and only the introduction of the sterlet into the Pechora (Barents Sea) and Western Dvina (White Sea) proved successful. Most attempts to introduce the rainbow trout and the brook trout into natural water bodies failed and these species established only rarely in nature. Some species are therefore maintained only, or predominantly in aquaculture facilities. This is the case for the rainbow trout, as well as all the three major Chinese herbivorous carps. These species are widely used throughout the Central and Eastern Europe in fishery farms and form some contribution to the aquaculture output of the Soviet Union, Romania, Germany, Hungary, Poland and Czecho-Slovakia. Even several tilapine cichlids have become aquaculture subjects during recent years in the Soviet Union, Czecho-Slovakia and even Belgium, where they are reared mainly in the heated power station cooling waters and sold occasionally in markets.

Risks of Introductions

In addition to the lack of apparent benefits, there are also cases of adverse or unexpected effects arising from introductions. For instance, it was observed that in both natural and man-made lakes, and in large channels stocked with grass carp the species composition of both macrophytes and phytoplankton changed dramatically, and the total catch of fish declined

TABLE 3. List of families, number of species, and number of receiving countries. Asterisk denotes family exotic for Europe. Arrangement of families according to decreasing number of species.

Family	Number of species (exotic/translocated)	Number of countries	Family	Number of species (exotic/translocated)	Number of countries
Cyprinidae	35 (14/21)	28	Umbridae	2 (1/1)	6
Salmonidae	17 (12/5)	28	Pleuronectidae	2 (–/2)	1
Coregonidae	11 (4/7)	12	*Anabantidae	1 (1/–)	1
*Cichlidae	10 (10/–)	8	*Channidae	1 (1/–)	2
*Centrarchidae	6 (6/–)	23	Clupeidae	1 (–/1)	1
Acipenseridae	5 (3/2)	8	*Eleotridae	1 (1/–)	1
*Poeciliidae	4 (4/–)	11	Engraulidae	1 (–/1)	1
Percidae	4 (1/3)	9	Esocidae	1 (–/1)	3
Mugilidae	4 (1/3)	1	Mullidae	1 (–/1)	1
*Ictaluridae	4 (4/–)	18	Osmeridae	1 (–/1)	1
*Catostomidae	3 (3/–)	6	*Percichthyidae	1 (1/–)	1
Gasterosteidae	3 (–/3)	5	Petromyzontidae	1 (–/1)	1
Anguillidae	2 (2/–)	3	*Polyodontidae	1 (1/–)	2
Atherinidae	2 (1/1)	2	Siluridae	1 (–/1)	6
*Clariidae	2 (2/–)	4	Syngnathidae	1 (–/1)	1
Gobiidae	2 (–/2)	2			
Thymallidae	2 (1/1)	3			

TABLE 4. List of countries, their area (A, km^2) and the number of species (n) they received. Number of exotic (numerator) and translocated (denominator) species is also shown.

Country	A	n	Country	A	n
USSR	5 443 900	70 (40/30)	Denmark	43 075	13 (9/4)
Italy	301 262	38 (26/12)	Austria	83 853	12 (9/3)
Czecho-Slovakia	127 889	36 (24/12)	Greece	131 944	11 (7/4)
Germany	356 330	29 (23/6)	Ireland	70 282	11 (6/5)
France	543 965	28 (21/7)	Sweden	449 964	11 (7/4)
Hungary	93 032	28 (22/6)	Bulgaria	110 912	10 (9/1)
UK	244 737	26 (17/9)	Portugal	91 631	9 (5/4)
Cyprus	9 351	22 (12/10)	Albania	28 748	9 (7/2)
Netherlands	41 160	21 (14/7)	Switzerland	41 293	8 (6/2)
Spain	504 783	20 (8/12)	Norway	323 920	7 (5/2)
Belgium	30 521	19 (12/7)	Luxemburg	2 586	2 (1/1)
Poland	312 683	18 (11/7)	Liechtenstein	157	2 (1/1)
Yugoslavia	255 804	18 (13/5)	Malta	316	2 (1/1)
Romania	237 500	15 (13/2)	Iceland	102 829	1 (1/1)
Finland	337 032	13 (18/5)			

significantly (Vinogradov and Zolotova 1974; Kogan 1974; Radziej and Krzywosz 1979; Krzywosz et al. 1980). Long-term observations made in one Danubian locality in Slovakia also revealed changes in the physical and chemical properties of the water (Holčík et al. 1985). The combined effect of these phenomena, initiated by the introduction of the grass carp, caused the density and biomass of fishes to decrease, in particular, those species (pike, common carp) whose reproduction invariably needs aquatic plants (Holčík et al. 1985). The rapid increase of the German carp (*Carassius auratus*) population, which invaded the lower and middle Danube in the late sixties and at the beginning of the seventies, is connected with the decrease of more valuable fish species, especially the common carp (Holčík 1980). Among the unexpected events, belongs the case of the exceptionally fast upstream invasion of the accidentally introduced Chinese cyprinid, *Pseudorasbora parva*. This species was discovered in one fish farm facility in Romania in 1960, but during next 24 years it was found in all the Danubian countries. Moreover, as a result of the stocking of other fish, especially the carp, it was also transferred to Germany, Albania and the USSR (Lithuania). It forms dense populations in some water bodies and it is blamed for strong food competition with other species and even for predation on their eggs and juveniles (Wohlgemuth and Šebela 1987). Pike (*Esox lucius*) and zander (*Stizostedion lucioperca*) introduced into Ireland and England are blamed for the eradication of salmonids and for the substantial decrease of some cyprinids (Fitzmaurice 1984; Linfield 1984). Nearly all North American centrarchids and ictalurids introduced to Europe are considered as pests and are blamed for predation on the eggs and young of native fish species. In some water bodies occupied by *Lepomis gibbosa* or by *Ictalurus nebulosus*, the native fish species were suppressed and their density decreased (Balon 1966; Adamczyk 1975; Danilkiewicz 1973). Introduction of the peled whitefish (*Coregonus peled*) led to hybridization with the native *Coregonus lavaretus* to such an extent that in 70% examined lakes in Poland, and in most fishery farms in Czecho-Slovakia, only the hybrids occur. It is suspected that because of this, some strains of *Coregonus lavaretus*, for example *C. lavaretus maraena*, probably do not occur more in their homeland (Holčík et al. 1989; Whitkowski 1989).

Introduction of diseases and parasites is also a problem intimately connected with introduction of fishes. Several new spe-

cies of parasites have spread into Europe as a consequence of fish transfers. The parasite fauna of Central Europe has increased, especially after the introduction of East Asian herbivorous carps, which — apart from their specific parasites — also carried several parasites which have affected the native fishes. For instance, these include the tapeworms *Bothriocephalus acheilognathi* (syn. *B. gowkongensis*) and *Khavia sinensis* which have become widely distributed in the fish farms of Hungary, Poland, Czecho-Slovakia and the USSR and are now the most significant pathogens in carp stocks (Žitňan 1974; Bauer 1975; Molnár 1984).

Conclusions

In conclusions, it may be stated that introductions of exotic species to Europe have brought controversial results. While there is no doubt as to the positive influence of some introduced fishes in aquaculture, the situation is much more complicated in natural water bodies. Although there is a vast amount of literature, especially in the USSR, dealing with the introduction of exotics into natural waters, there is a lack of any serious, impartial and generally valid evaluation of introduction experiments based on thorough ecological analysis. Moreover, a vast amount of data and information concerning introductions are of variable value. For instance, one is unable to judge whether any increased catch of fish in some water bodies is due to introductions or due to changes in fishing effort (Holčík 1984). In addition, there are indications that the success of acclimatization experiments is often exaggerated, in that the actual results do not correspond with those which are proclaimed (Holčík 1984), and that there are also serious shortcomings and adverse effects (Markevich 1978; Myagkov 1990), which are usually not published. However, one fact remains certain: only few species are generally accepted as having been beneficial introductions. From native species there is a common carp, and in some countries also the zander, and one or two coregonids. From the exotic species it is the rainbow trout which received a good reputation everywhere, along with Chinese herbivorous carps.

As a result of the dangers and risks caused by introductions, many European countries have introduced measures to control them. However, it is essential that unified regulations are developed, as at present they differ among countries. It is recommended, therefore, to accept the Code of Practice adopted by the European Inland Fishery Advisory Commission in 1987 as the most useful tool for the regulation and international control of fish introductions.

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Impacts of Fish Introductions in Tropical Asia and America[1]

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Biotas are constantly being reshaped by invasions. Introduction is now an added route to invaders. Impacts must be viewed against the background of massive changes in type, extent and quality of freshwater habits globally and in that freshwater fishes are almost living fossils. Also, old lakes and lacustrine fishes are highly restricted geographically. Lakes are young while rivers are old. Riverine, marsh and pond fishes are not well adapted to lacustrine conditions now widespread due to reservoir construction. Some Clupeidae and Cichlidae are lacustrine-adapted and highly productive. They have therefore made major impacts on fish yields in lakes and reservoirs. In tropical Asia and America, there have been a series of overlapping waves of fish introductions during the past 150 years, culminating tin the tilapias from Africa. These fishes now dominate capture and culture fisheries in many countries. Fish introductions are a fait accompli and will continue. They must be realistically assessed and carefully monitored. Contrary to some predictions, introductions have not caused severe damage to indigenous species except when piscivores were used. Yields of indigenous fishes have apparently been enhanced in some instances. Parasites pose a serious threat and only an effective quarantine will ensure their exclusion.

Les biocénoses sont constamment modifiées par les invasions. L'introduction constitue maintenant une autre voie d'invasion. On doit examiner globalement l'impact de l'introduction d'espèces étrangères en fonction des nombreux changements qui surviennent dans la nature, l'étendue et la qualité des habitats d'eau douce, et en tenant compte du fait que les poissons d'eau douce sont presque des fossiles vivants. De plus, les poissons peuplant les vieux lacs sont très limités géographiquement. Les lacs sont jeunes comparativement aux rivières. Les poissons de rivières, de marais ou d'étang sont mal adaptés aux conditions lacustres qui sont maintenant répandues en raison de la construction de réservoirs. Certaines espèces de Clupeidae et de Cichlidae sont adaptées aux conditions lacustres et ont une productivité élevée. Par conséquent, elles ont eu des effets importants sur les récoltes de poissons dans les lacs et les réservoirs. En Asie et en Amérique tropicales, on a procédé au cours des 150 dernières années à l'introduction de poissons par vagues qui se chevauchent et qui a culminé par l'introduction de tilapias originaires d'Afrique. Dans de nombreux pays, ce poisson constitue maintenant la principale espèce pêchée et élevée. L'introduction de poissons est devenue une situation de fait qui est là pour rester. Il faut qu'elle soit évaluée de façon réaliste et surveillée rigoureusement. Contrairement à certaines prévisions, l'introduction de poissons n'a pas affecté gravement les espèces indigènes, sauf lorsqu'il s'agissait de l'introduction d'espèces piscivores. Dans certains cas, le rendement des espèces indigènes semble s'être amélioré. Les parasites représentent une menace importante et seules des mesures de quarantaine efficaces garantiront leur exclusion.

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Fish introductions must be viewed as continuing invasions which now form an integral part of the evolution of biotas. The impacts of fish introductions must be set against the background of massive global changes caused by human activities. For example, the construction of reservoirs has accelerated immensely during the past 50 years. Already reservoir areas outstrip the area of natural lakes except in limited areas of the glaciated Northern hemisphere and the rift valley in Africa. In fact the lacustrine habitat which was very restricted globally, is now almost ubiquitous (Fig. 1). Besides the damming of river systems for reservoir construction, human induced changes affect the type, extent and quality of freshwater habitats and also involves the conversion of marshes into ricefields and the reclamation of wetlands for industry, habitation and road building. All these activities and accompanying eutrophication and other forms of pollution have profound impacts on the diversity and composition of fishes and other aquatic biota. The pressure for increased fish production, the need to control nuisance organisms and vectors of disease, the demand for recreational sport fishing and indoor ornamental fish have fuelled fish introductions at an accelerating pace in recent years.

Most groups of animals show distinct variations in latitudinal diversity. Fishes are no exception to this rule. However, freshwater fishes which comprise a highly skewed 40% of the 20 000 global fish species, are nevertheless almost living fossils because of their slowness in colonizing new areas as Elton (1958) has remarked. Rivers are old and have diverse fish faunas. An exception seems to be the Australasian rivers as exemplified by the Sepik in Papua New Guinea (Coates 1987). On the other hand, lakes are young with very few exceptions and these together with reservoirs do not have diverse or lacustrine fish faunas. Old lakes with lacustrine fish faunas are few and isolated, e.g., L. Baikal and L. Tanganiyka (Fernando and

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FIG. 1. Global distribution of lakes, reservoirs and freshwater fishes. Cl = Marine Clupeidae L with arrow, = many lacustrine fishes including fish flocks 1 = small number of lacustrine fishes (slightly modified from Fernando 1991).

Holčík 1982, 1989, 1990). Recruits to lakes and reservoirs are drawn from rivers and to a lesser extent perhaps from ponds and marshes. Marine fishes have also invaded the lacustrine environment and have given rise to secondary freshwater fishes like the Cichlidae and Centropomidae and marine intruders like the Atherinidae and Galaxidae. Among the marine intruders, the Clupeidae are the most productive. They are established in some old lakes like L. Tanganiyka, colonize reservoirs via river systems, as on the Dnieper, or have been introduced into lakes and reservoirs (Fernando and Holčík 1990; Spleithoff et al. 1983). They occur now in lacustrine habitats on all continents (Fig. 1).

Against this backdrop of massive, pervasive, and worldwide human impacts on freshwater habitats, the slowness of movement of freshwater fishes and the isolation and relatively limited diversity (except in the rift valley area) of lacustrine fishes, introduction of fishes has had only very modest effects on the indigenous fish faunas, while raising fish yields considerably. The negative impacts of fish introductions have been due to piscivores mainly and the transfer of disease causing organisms. Some instances of stunting in "*r*" strategists are known too. These are discussed later. Fish faunas have been diversified and poorly used portions of habitats have been used effectively by introduced fishes. More study is needed on the apparent increase of indigenous fish stocks, especially Cyprinidae due to the presence of herbivorous tilapias.

Early Introductions and Broad Impacts

Fishes were certainly moved across distances in ancient civilizations. Welcomme (1988) lists 7 species in this category from Asia, Europe, North America and Oceania. Kottelat (1990) refers to the introduction of *Clarias* by Javanese transmigrants into Sulawesi and mentions the probability that *Anabas testudineus* and *Channa striata* were introduced to the same area. All these species are air breathers and can survive overland travel under primitive conditions. The impact of these early introductions is difficult to assess now, although Kottelat (1990) attributes disease transfer and the presence of *Clarias* for the decline of indigenous fish populations in Sulawesi.

During the past 150 years or so, the enterprise, if it may be called that, of fish introductions has accelerated (Welcomme 1988). Side by side with this increase in the successful transfer of fishes there has been a concomittant increase in the impact of higher human densities, industrialization, interference with, and alteration of freshwater habitats globally and other anthropogenic changes. The effects of fish introductions and other human impacts cannot be separated. However, there have been overlapping waves of fish introductions. The factors that have influenced this pattern and the choice of species include political changes, human migrations, familiarity and various economic motives like sport, food, control of other organisms and ornament. Accidental introductions account for about 10% of the species involved (Welcomme 1988).

Introductions in Tropical Asia and America

There is an extensive literature on fish introductions in these areas. This is however a great deal of controversy as to the impacts of these introductions. I shall attempt to provide both a perspective of the extent of introductions and their impacts.

In the past 150 years or so, fish introductions into the tropics can be considered as a series of overlapping waves. Like colonialism which affected the tropics via the North temperate zone during this period, fish that reached Asia and America in the first wave came from the North temperate zone. Familiarity was a major reason for the choice of particular species. Since tropical lowlands were not particularly suitable for temperate fishes, and lacustrine fishes are rare in the temperate zone, upland streams provided the only suitable sites for introduction of fishes. These introductions were largely of piscivorous sport fishes like trout and bass. Rivero (1927) recorded the destructive impact of these fishes in subtropical Cuban freshwaters. There is little doubt that there was a similar impact in other parts of the subtropics and tropical highlands, both in Asia and America. The tolerant common carp was also introduced and survived. This sport fishery is now of negligible importance. The efforts to establish north temperate piscivores and carnivores has been continued and successful introductions have been made to Lake Titicaca (Peru–Bolivia) and Lake Atitlan (Guatemala) with predictable destructive effects on the indigenous fish faunas and catastrophic effects on the artisanal indigenous fisheries (Dorris and Summerfelt 1968; Laba 1979). Bass were introduced into Lake Lanao (Frey 1969) but mercifully died out. Lake Lanao also received tropical piscivores accidentally. These fishes had a marked negative impact on indigenous fishes and fisheries (Frey 1969; Kornfield 1982). However, we should be cautious in accepting reports on the elimination of indigenous fish. Recently, Kottelat (1990) cautioned against accepting anecdotal evidence or those reports of extinctions based on insufficient and inefficient collecting. The impact of water level changes notwithstanding, fish introductions in Lake Lanao in addition to cage culture (presumably), has increased the fish yield to 286 $kg \cdot ha^{-1}$ in 1986 from 46 $kg \cdot ha^{-1} \cdot yr^{-1}$ before introductions. The status of the endemic fish flock of Cyprinidae is not clear though some loss of species is feared (Baluyat 1986; Frey 1969; Kornfield 1982). Welcomme (1988) reported the recolonization by native fish of an area in Gatun Lake, Panama, where they were supposed to have been eliminated (Zaret and Paine 1973), indicating that one should be cautious about predicting extermination.

Fish introductions into Indian freshwaters is illustrative of what has happened throughout Asia. Jones and Sarojini (1952) listed and discussed early fish introductions. Their list of species included the intra-Indian transfer of major carps and sport fishes and in addition, European carps, *Cyprinus carpio, Carassius carassius* and *Tinca tinca*. All these temperate species were moved to tropical regions. Tropical intra-Indian transfers included the piscivorous *Ophiocephalus* and the herbivorous estuarine cichlid *Etroplus suratensis*; others included *Osphronemus goramy* from Indonesia and *Oreochromus mossambicus* from Southern Africa. They also mentioned larvivorous fishes like *Gambusia affinis* and ornamentals accidentally released.

Fernando (1971) recorded 15 introduced species in Sri Lanka excluding larvivores and ornamentals. A listing of fishes introduced into most Asian countries is available in De Silva (1989). The summarized assessment of their impacts is that Asia has suffered few losses of native species to introductions. There was a note though of caution against complacency about fish introduction and a plea for regulation. In sharp contrast to this assessment is the loss of 38 of Singapore's 70 freshwater fishes (Alfred 1961). Presumably, this loss is a result of urbanization.

I wish to turn to two groups of herbivorous (and omnivorous) fishes introduced widely in tropical Asia. One of these groups comprises extra-tropical carps which do not usually reproduce naturally in tropical waters. These include the Indian, Chinese and common carps. Their impact on fish yields has not been

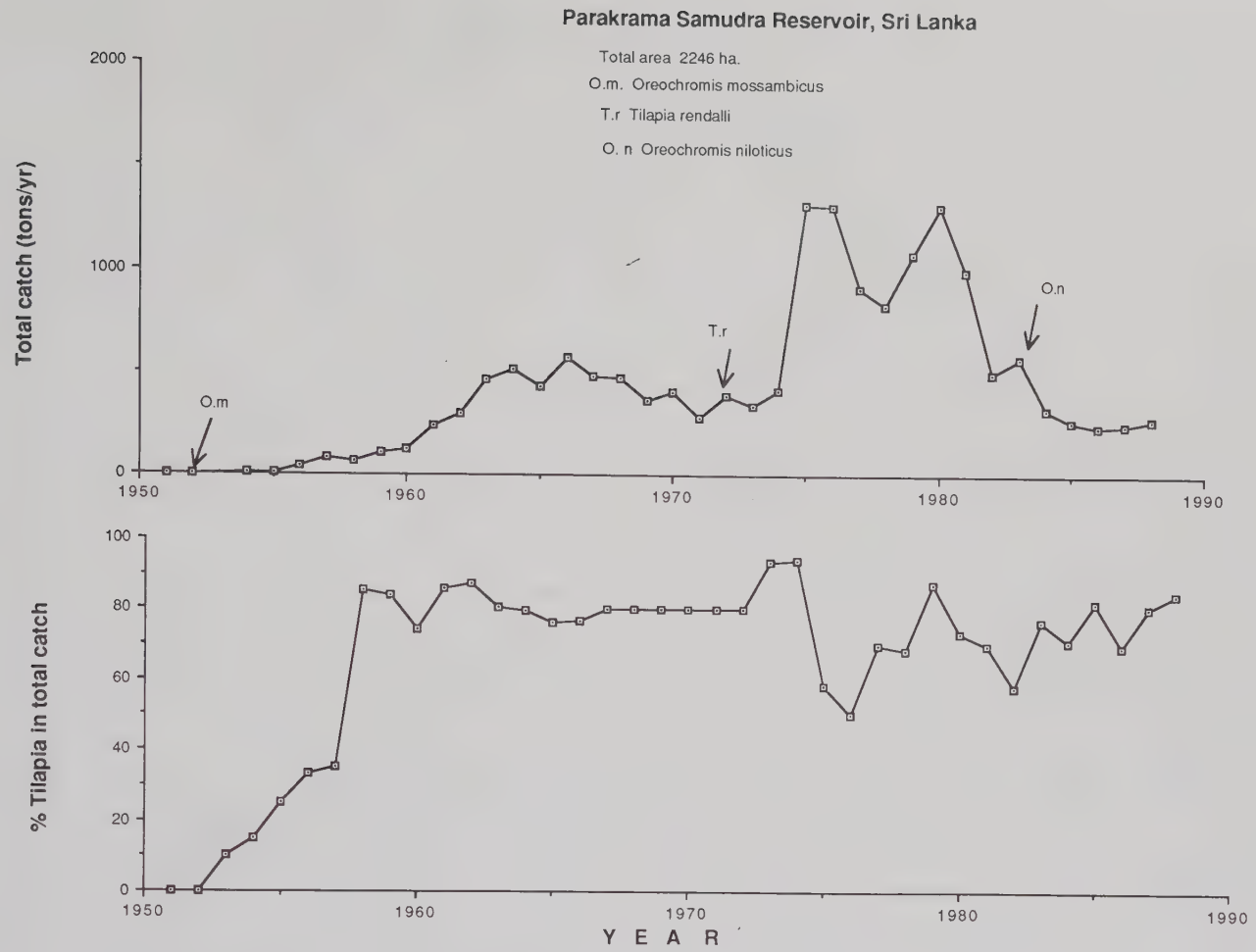

FIG. 2. Fish yields in Parakrama Samudra, an ancient reservoir in Sri Lanka. Data from Fernando (1991).

negligible but they are costly to cultivate and their use in the tropics is diminishing. They have the advantage that they do not breed in tropical waters but they are uneconomic. In Sri Lanka *Cyprinus carpio* has been stocked in reservoirs for 45 years with no economic return, while in Southern Indian reservoirs there is a negative regression between common carp and the total fish yield (Fernando and Holčík 1990). In Thailand exotic carps and *Oreochromis niloticus* have been stocked into reservoirs, the former at considerable cost (Bhukaswan 1989). According to Bhukaswan and Chookajorn (1985) only *O. niloticus* has contributed significantly to the reservoir fish catch. Bhukaswan (1989) was unable to show a positive economic return from exotic carp stocking in Thai reservoirs. In 1986, 23 000 tons of *Oreochromis* were caught while only 4 000 tons of stocked common carp were caught. No other exotic carps were reported (Statistics, Department of Fisheries in Bangkok, Thailand, 1987). Thus it appears that attempts to use them to stock lakes and reservoirs has not been successful economically. The second group of exotics includes tropical species. Species introduced within Asia include the gourami's, carps and cichlids. None of these have so far had a major impact on either capture or culture fisheries. The tilapias (Cichlidae) from Africa have been widely dispersed since the fifties. Their impact on both capture and culture fisheries in tropical Asia has been spectacular. Sri Lanka, which had no noteworthy inland fishery before tilapias, now harvests 25 000 – 30 000 tons from reservoirs, representing 300 $kg \cdot h^{-1} \cdot yr^{-1}$ as a mean value for about 100 000 ha of larger shallow reservoirs. The fish catches from one such reservoir, Parakrama Samudra is shown in Fig. 2. Indigenous fishes have not been negatively affected. On the contrary, it appears that they have benefited from the presence of tilapias (De Silva and Fernando 1980). It appears likely that the high densities of tilapias speeds up mineralization thus enhancing plant growth. Cyprinidae, which comprise most of the indigenous fish component in the catch, benefit from eutrophication (Trevino et al. 1989). Parakrama Samudra supports a very dense fish eating bird population (Winkler 1983) and also indigenous piscivorous Siluridae and Channidae. Tilapias probably reduce predation pressure on indigenous cyprinids. These factors could contribute to enhanced yields of indigenous carps. Increased exploitation alone, as has been suggested by some, does not seem a likely reason for an increase of such magnitude in the yield of indigenous cyprinids. Based on an extensive study of cichlids and fisheries in African lakes and reservoirs, Fryer and Iles (1972), state that the very presence of a species of tilapia makes an important contribution to the fish production of a lake. This is besides the yields of tilapias.

In tropical India where tilapias are not considered desirable, reservoir management includes regular stocking with extra-tropical carps. The fish yields are about 20 $kg \cdot h^{-1} \cdot yr^{-1}$, but when present, tilapias enhance fish yields while common carp seem to depress yields (Fig. 3 and 4). In Jatiluhur reservoir, Indonesia, tilapias dominate the catch and have a positive impact on yields (Fig. 5). In this case though the fish yield is

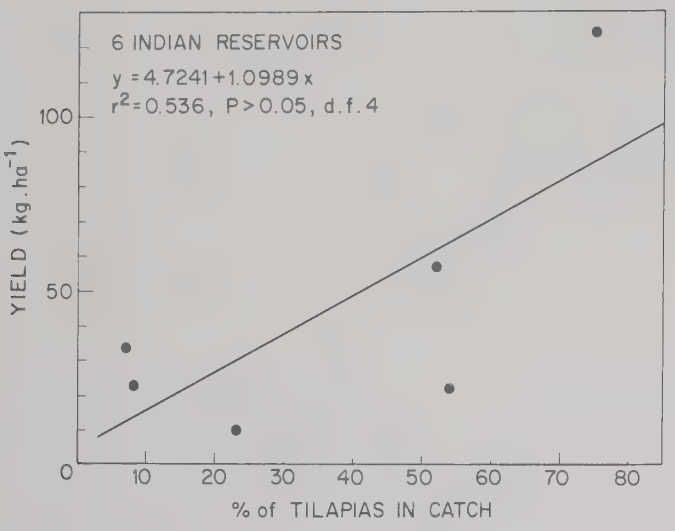

FIG. 3. Fish yields for Indian reservoirs showing the relationship between fish yields and tilapias (after Fernando and Holčík 1990).

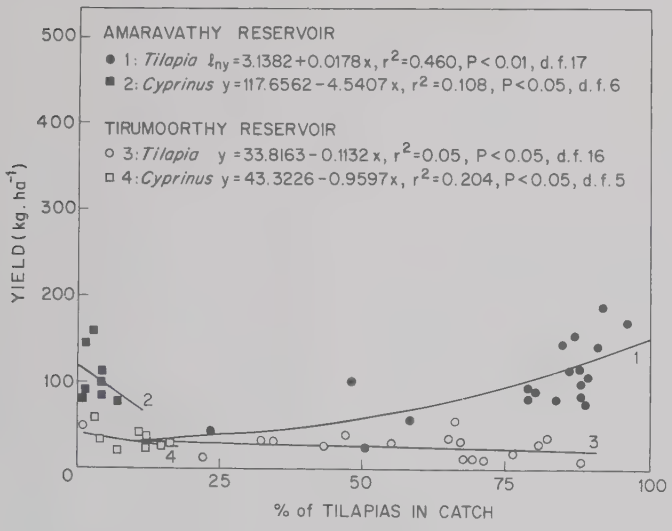
AMARAVATHY RESERVOIR
1: Tilapia ℓny = 3.1382 + 0.0178 x, r² = 0.460, P < 0.01, d.f. 17
2: Cyprinus y = 117.6562 − 4.5407 x, r² = 0.108, P < 0.05, d.f. 6
TIRUMOORTHY RESERVOIR
3: Tilapia y = 33.8163 − 0.1132 x, r² = 0.05, P < 0.05, d.f. 16
4: Cyprinus y = 43.3226 − 0.9597 x, r² = 0.204, P < 0.05, d.f. 5
YIELD (kg.ha⁻¹)
% of TILAPIAS IN CATCH

FIG. 4. Fish yields in two Indian reservoirs. In Amaravathy reservoir, the catch is dominated by tilapias while in Tirumoorthy reservoir tilapias do not figure prominently in the catch. The role of common carp in both reservoirs seems to be negative on fish yields (after Fernando and Holčík 1990).

only about 15 $kg \cdot h^{-1} \cdot yr^{-1}$. Jatiluhur reservoir is deep and not productive due to this reason and the turbid water which reduces primary production. In Thailand, tilapias play a part in capture fisheries. In 1987, 24 000 tons was landed (Data from Dr. T. Bhukaswan). In Ubolratana reservoir (41 000 ha, mean depth 16 m) where tilapias are still insignificant, the fish yield is only about 40 $kg \cdot h^{-1} \cdot yr^{-1}$. Of this, about 70% consists of Cyprinidae, while 10% is a sardine *Clupeichthys aesarnensis* (Fig. 6). Shallow reservoirs similar though admittedly not strictly comparable to Ubolratana reservoir but with tilapias, give fish yields over 100 $kg \cdot ha^{-1} \cdot yr^{-1}$ in Sri Lanka and tropical Africa (Fernando and Holčík 1982). Tilapias have had a remarkable impact on tropical Asian capture fisheries raising yields which are 20–40 $kg \cdot ha^{-1} \cdot yr^{-1}$ with indigenous species in shallow reservoirs to more than 10 times that figure under favourable conditions. It is, however, in culture that the role of tilapias is even more spectacular. This fish is replacing carp

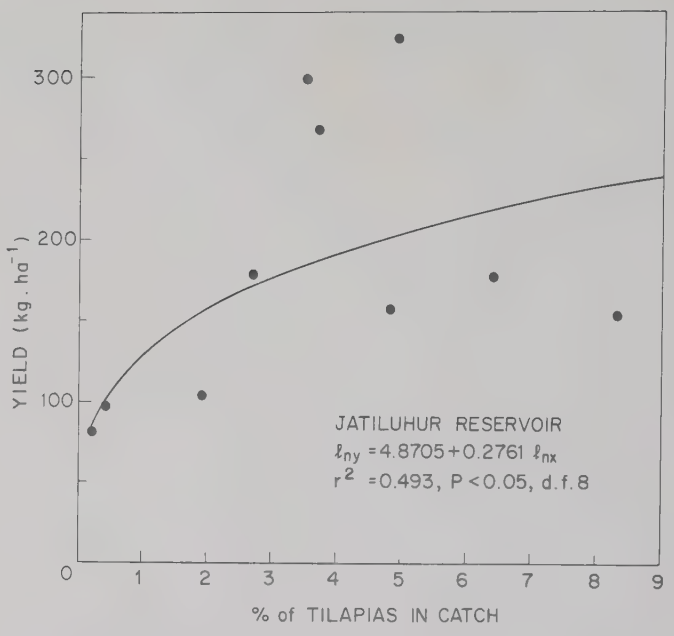

FIG. 5. Fish yields in Jatiluhur reservoir, Java, Indonesia. The fish dominating the catch are tilapias and carnivores (after Fernando and Holčík 1990).

and milkfish culture in Philippines, Thailand, Indonesia and Taiwan. In Taiwan, the ratio of tilapia to milkfish in culture fisheries has changed from 28 to 174% between 1969 and 1982. *Oreochromis* in culture contributed 51 000 tons in 1982 compared to 26 000 tons of common carp and 29 000 tons of milkfish (Kuo 1984). Costa-Pierce et al. (1988) record the replacement of milkfish by *Oreochromis* in Philippine fish culture, where tilapias are second only to milkfish in tonnage of culture fish produced. In Indonesia tilapias have sometimes replaced milkfish in culture fisheries (D. Rustami, pers. comm.). On the negative side, tilapias are said to become stunted but this phenomenon is rare. There is anecdotal evidence cited that they damage milkfish culture (Chandrasekeran and Sreenivasan 1988) and damaged a gobi fishery (Gindelberger 1981). The drawbacks of tilapias are relatively minor compared to their contribution to the fisheries in Asia. However, tilapias have been branded unequivocally as pests by Arthington (1988) while Lowe-McConnell (1987) wrongly restricts their positive impacts on fisheries to only a few places in the tropics. In a subsequent paper Blühdorn and Arthington (1990), the declaration of pest status was restricted to Queensland, Australia.

In tropical America, the same pattern of fish introductions has occurred as in the Asian tropics. However, there are differences in the timing, and the species used. The composition of indigenous fish faunas, and the practice of aquaculture are also different. Tropical South America has a rich indigenous riverine fauna (Fig. 1). Central America on the other hand has a very limited fauna of primary freshwater fishes (Myers 1966). Fish introductions came later to tropical America than to Asia. The earliest introductions were of sport fishes followed by extratropical carps for culture and the intra-American transfer of species. The impact of piscivorous fishes has been documented for Cuba (Rivero 1927) and Mexico (Contreras and Escalente 1984). This negative impact on indigenous fishes can be considered general for tropical America. Bonetto and Castello (1985) list the species introduced. It is clear that piscivores are

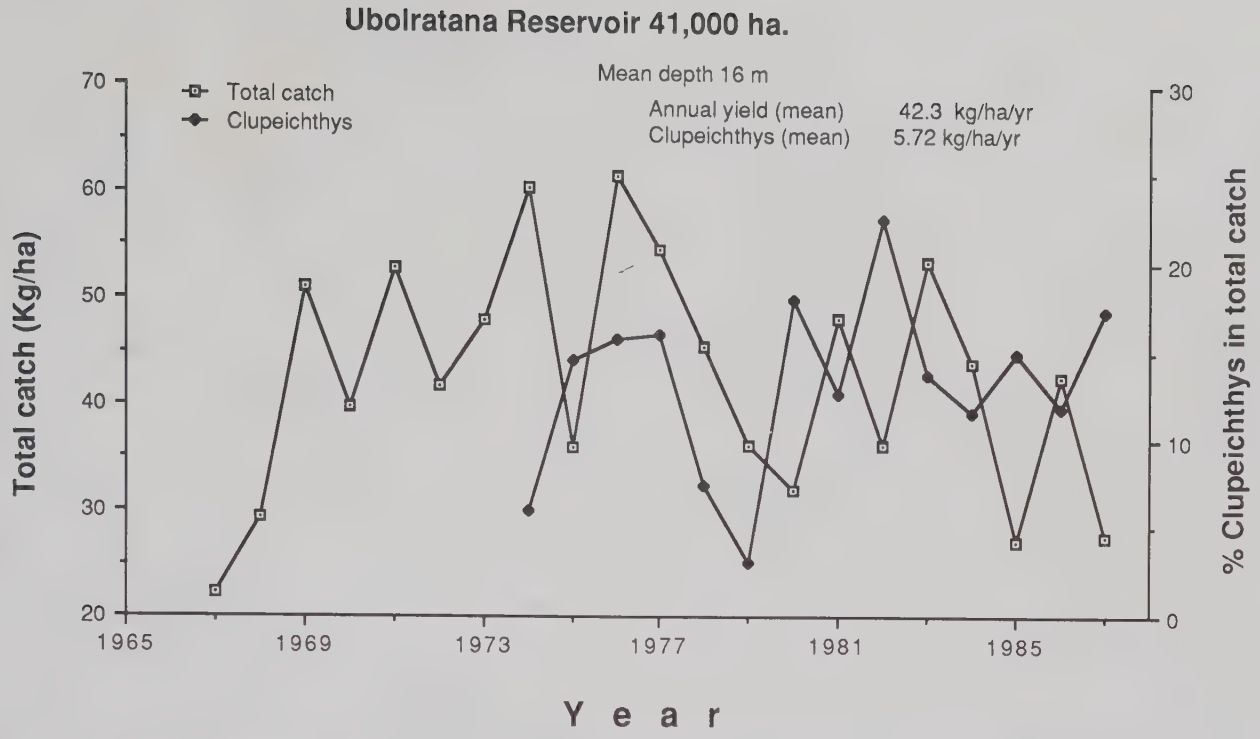

FIG. 6. Fish yields in Ubolratana reservoir in Thailand. Tilapias do not figure in the catch prominently although they are present. Data sorted out by Ms. Renu Sirimongkonthaworn from statistics published by the Fisheries Department Bangkok, Thailand.

predominant. This is a sharp contrast to Asia where herbivores and omnivores comprise the majority of introduced species. In addition, we have the specific cases of L. Titicaca (Laba 1979), L. Atitlan (Dorris and Summerfelt 1968) and Gatun Lake (Zaret and Paine 1973) where piscivores have had a negative impact on the indigenous fishes. For Northeast Brazil we have a well documented account of both the sequence of fish introduction and the changes in the fisheries in reservoirs (Gurgel and Oliviera 1987). Local, Amazonian and foreign species of fish were introduced and the fish yields in reservoirs is substantial. Tilapias contribute about 30% of the catch in DNOCS reservoirs (Fig. 7). In Mexico, the inland fish catch which comes mainly from reservoirs consisted of 65–72% of tilapias in the years 1983–85 (Anon. 1986). In Lake Chapala, the largest natural lake in Mexico, 70% of the 26 $kg \cdot h^{-1} \cdot yr^{-1}$ catch consists of tilapias (Dr. G. Arroyo, pers. comm.). In Miguel Aleman reservoir, Mexico, a fish yield of 40 $kg \cdot ha^{-1} \cdot yr^{-1}$ (Fig. 8), consists mainly (90%) of tilapias. In the Dominican Republic 76–90 of the modest inland fish catch consisted of tilapias (Anon. 1980). Holčík (1970) studied fish production of some Cuban lakes and noted that the indigenous (aboriginal) fishes, or what was left of them after decimation by bass, had a low production compared to introduced bass and sunfish. In Cuba the mean annual catch of tilapias for 1970–74 was 14 tons, from 1975–79 it was 543 tons and from 1980 to 1984 it was 9 967 tons. Tilapias accounted for 9 967 tons or 93% of the total catch of all species for 1980–84 from inland waters of a total of 10 659 tons. The catches of other species had actually increased from 269 tons for 1970–74 to 692 tons for the period 1980–84 (Diaz et al. 1988). Dr. Len Lovshin who has worked on inland fisheries in Brazil and Panama stated in a letter that the relative lack of success of tilapias in tropical America was due to high predation by indigenous piscivores. This is generally true. Lowe-McConnell (1969) found that tilapias were eliminated from Guyana sugarcane field ditches by predatory fishes. In Thailand, Ling (1953) attributed the elimination of tilapias to fish predators. However, the establishment of tilapias a a substantial contributor to the fisheries in Northeast Brazil and their prominence in fisheries in some other tropical American countries indicates that they can successfully weather predation. Even in Thailand tilapias are now prominent in capture fisheries. Dr. T. Bhukaswan, Bangkok, (pers. comm.) gives a figure of 24 000 tons for 1987.

Myers (1955) predicted dire consequences if tilapias were introduced into Central America. He based this statement neither on previous evidence nor on a first hand study. Riedel (1965) who studied the impact of tilapias in Nicaragua came to the opposite conclusion and suggested their introduction to enhance fisheries. Time has proved that Myers' (1955) fear was groundless.

In tropical America as in Asia, piscivorous fishes have caused a negative impact on indigenous fishes. The role of exotic sport fishes and extra-tropical herbivores and omnivores remain negligible. Tilapias on the other hand have made substantial introductions to the fisheries and apparently have caused no harm to indigenous fishes.

Disease Transfer

An ever present hazard in fish introductions is the transfer of parasites to indigenous fishes and subsequent outbreaks of epizootics both in wild and cultured fishes. In the wild, diseases are seldom reported. However, recently, Wurtsbaugh and Tapia (1988) recorded a mass mortality of fish in Lake Titicaca due to an introduced protozoan, *Ichthyopthirius multifillis*. Fernando and Furtado (1963) reported a cestode, *Bothriocephalus acheilognathi* from Chinese carps in an indigenous carp in Sri Lanka. Kabata (1985) recorded a number of introduced parasites in cultured fishes in some South East Asian countries.

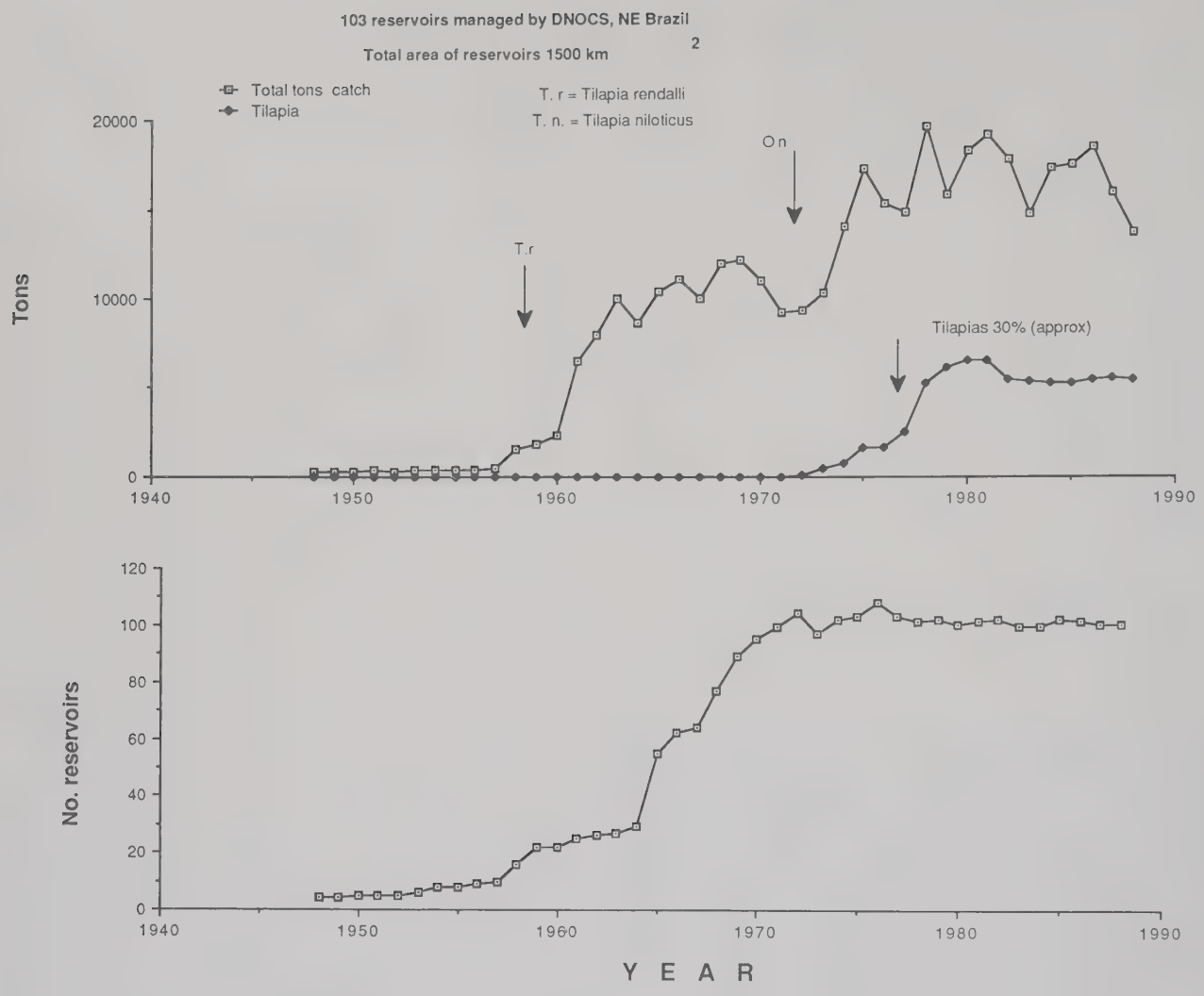

FIG. 7. Fish yields in DNOCS controlled reservoirs in Northeast Brazil. Data supplied by Drs. José William Bezerra e Silva and J. J. S. Gurgel.

Fernando and Hanek (1973) reported that 3 of the 7 Copepoda parasitic in freshwater fishes in Sri Lanka had been introduced into that country with fish brought in for culture from abroad. There is no way to assess comprehensively the extent of introduction of fish parasites in capture and culture fisheries from the data available. Also, many fish parasites have stages in birds which migrate across wide areas and thus these parasites invade new areas on a regular basis. It can perhaps be stated that due to the transfer of fishes, some parasites like *Lernaea cyprinacea* and *Argulus foliaceus* have become cosmopolitan thanks to carp culture. Hoffmann (1967) and Kabata (1985) record both these North Eurasian cyprinid parasites outside this region. Kabata (1985) found the records of *A. foliaceus* confined to common carp in culture and Hoffman (1985) records *A. foliaceaus* as cosmopolitan. Disease causing organisms are among the major risks of any transfer of fishes. Quarantine can keep some of these out but already there has been a transfer of many such organisms to new locations.

Discussion

While the past 150 years has seen the introduction of a wide range of freshwater fishes both within and across zoogeographic regions, the impact of these introductions have not been spectacular except in a few cases in tropical Asia and America. On the other hand, the changes wrought in the type, nature and extent of freshwater habitats by human activities has been pervasive and profound. The creation of large areas of standing waters in the form of reservoirs in areas with only riverine, pond and marsh habitats is one of the most widespread human enterprises. This enterprise of reservoir construction among other impacts must be taken into account when the impacts of fish introductions are assessed for positive and negative impacts.

On the negative side of fish introductions, the elimination or decimation of indigenous fishes is the most serious in the long-term. This impact is often attributable to introduced piscivorous fishes besides other human induced changes. In regions where the indigenous fish fauna is depauperate as in Cuba, Central America, or in Lake Lanao, Philippines, these introductions can be catastrophic. However, the impact of the introduced fish cannot be separated from the effects of other anthropogenic effects.

A case can be made for the introduction of lacustrine and lacustrine adapted fishes into reservoirs where lacustrine fishes are missing from the indigenous fish component as in Northeast

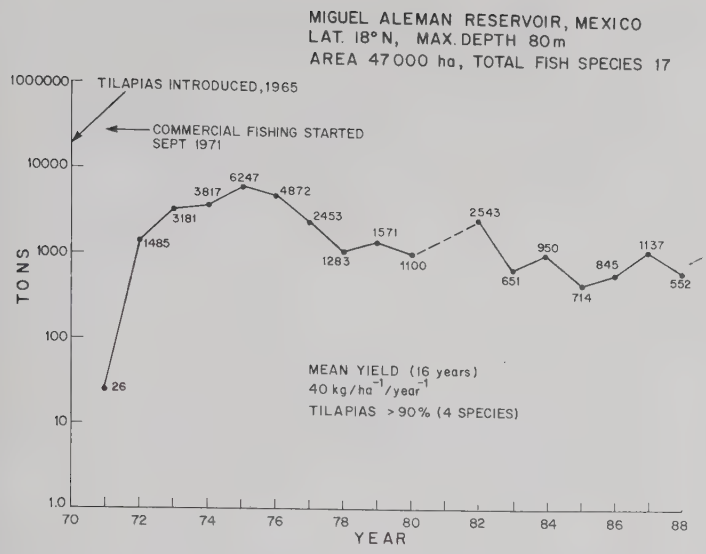

FIG. 8. Fish yields in a Mexican reservoir. Data from Fernando and Holčík 1985 and 1982–88 data from Senor Marcelo Silva Briano, Aquascalientes, Mexico.

Brazil and Sri Lanka. During a period of almost 40 years, no negative impacts have been noted in these two cases. This result could have been predicted on common sense and simple biological principles. Omnivorous fishes were used in Sri Lanka. In Brazil, omnivores and piscivores were used. There were no indigenous fishes which could occupy the newly created class of habitats adequately to provide the high fish yields presently obtained.

The high yields of non-tilapias when tilapias are present is well known (Fryer and Iles 1972). Cyprinidae seem to benefit from the presence of tilapias as mentioned earlier. This may give the false impression that tilapias are not essential to give high fish yields in shallow tropical lakes and reservoirs.

Bates (1956) in his study of man as an agent in the spread of organisms makes a plea for the study of experimental-like situations produced by human alteration of the environment, including introduction of organisms. There are opportunities in such situations, he said, for the understanding of ecology in general and also some key aspects of the ecology of organisms and the possible mechanisms of organic evolution. Fryer (1990) is sceptical about theoretical pronouncements and modelling as predictive tools in assessing introductions. Chance, rather than genetic attributes alone, seems to be more important to invaders as Gould (1989) has shown recently for the early evolution of invertebrate groups. The absence of old lakes has precluded the evolution of lacustrine fishes over most of the globe. The creation of reservoirs provides the habitat but not the preadapted inhabitants nor the requisite time. When the necessary components of lacustrine conditions and suitable fish are brought together, there is success for the introduced fish (Fernando and Holčík 1982, 1985, 1989, 1990). The claim that indigenous riverine fish will be just as successful in providing high fish yields in lakes and reservoirs has been put forward by De Silva (1988). The data available globally however indicates that this is not likely. Even where riverine fish like Cyprinidae have occupied lacustrine situations for a long time as in Lake Lanao and the pelagic of Lakes Malawi and Lake Victoria, the fish yields they give are lower than that of lacustrine and lacustrine adapted fish like tilapias and clupeids.

Bates (1956) makes the statement that the larvivorous fish *Gambusia* seem nowhere to have caused any disasters. However, he was not able to obtain clear proof that they have reduced malaria either, the reason for their introduction. Such causal connections are difficult to make without comparative studies and no two situations will be sufficiently close for valid comparisons. I think we will face similar difficulties in assessing the positive and negative impacts of other fish introductions. The problem is further complicated by differences of opinion as to whether a particular fish like tilapia is a pest or an important food item. If there is an inherent bias against the introduction of alien species of fish then there will be a search only for the negative impacts of fish introductions. I was quite surprised to find that Elton (1958) had quite an open-minded approach to exotics. He advocated reconstruction of biotic communities and included suitable exotics as part of this enterprise because exotics, he said, would get there anyway.

Fish introductions into tropical freshwaters in Asia and America have had a wide range of impacts. These impacts though are difficult to ascribe to the fish only, since major changes in the nature, extent and type of freshwater habitats have been caused by human intervention. There do not appear to be any ironclad rules about the choice of species or whether fish should be introduced at all. We must look as objectively as possible at the experience of fish introductions and use common sense and sound biological principles in judging suitability or otherwise of introductions.

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Ecological and Genetic Impacts of Introduced and Translocated Freshwater Fishes in Australia[1]

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Arthington, A. H. 1991. Ecological and genetic impacts of introduced and translocated freshwater fishes in Australia. Can. J. Fish. Aquat. Sci. 48 (Suppl. 1): 33–43.

The inland waters of Australia have been colonized successfully by 20 species of freshwater fishes introduced to the continent, including 6 poeciliids, 3 salmonids, 4 cyprinids, 5 cichlids, 1 percid and 1 cobitid, all of which reproduce there in the wild. The ecological and genetic consequences of fish introductions and translocations have concerned scientists and water authorities since the late 1960's, although the earliest introductions of salmonids for sport were made towards the end of the 19th century. Impacts of introduced fishes, including hybridization problems, habitat and water quality alterations, competition for space and food, predation and the introduction of exotic parasites and diseases are reviewed. Emphasis is placed on sub-tropical and tropical species, since they appear to present the greatest threat to natural ecosystems. Problems in the translocation of indigenous Australian fishes between drainage systems to supplement recreational fishing are noted; a review of the Lake Eacham rainbowfish, supposedly brought close to extinction in its natural habitat by translocated Australian piscivores, demonstrates that unanticipated predator–prey interactions may result from the thoughtless addition of piscivores to an endemic community. A theoretical perspective on the assessment of candidate species for introduction and translocation is given, and areas of theoretical ecology that may assist in predicting future impacts of introduced species are discussed.

Les eaux intérieures de l'Australie ont été colonisées avec succès par 20 espèces de poissons d'eau douce introduites dans ce continent (6 Poeciliidae, 3 Salmonidae, 4 Cyprinidae, 5 Cichlidae, 1 Percidae et 1 Cobitidae) où toutes ont établi des stocks viables. Depuis la fin des années 60, les scientifiques et les responsables de la gestion des eaux se sont intéressés aux conséquences écologiques et génétiques de l'introduction et de la transplantation de poissons, bien que les premiers cas d'introduction de poissons pour les besoins de la pêche sportive remontent à la fin du XIX^{e} siècle. On passe en revue les effets de l'introduction de poissons, y compris les problèmes d'hybridation, les modifications de l'habitat et de la qualité de l'eau, la compétition pour l'espace et l'alimentation, la prédation et l'introduction de parasites et de maladies exotiques. L'accent est mis sur les espèces tropicales et subtropicales, car elles semblent représenter la menace la plus importante pour les écosystèmes naturels. On indique les difficultés liées à la transplantation, d'un bassin hydrographique à un autre, de poissons indigènes pour soutenir le rendement de la pêche récréative; une analyse portant sur le poisson arc-en-ciel du lac Eacham, qu'on a cru presque éliminé de son habitat naturel à la suite de la transplantation d'espèces piscivores provenant d'autres régions de l'Australie, démontre que l'introduction irréfléchie d'espèces piscivores dans une communauté endémique peut provoquer des interactions prédateur–proie imprévues. On présente une perspective théorique sur l'évaluation d'espèces candidates pour l'introduction et la transplantation et on discute des champs de l'écologie théorique qui peuvent s'appliquer à la prévision des effets de l'introduction.

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Inland waterways, lakes and wetlands of mainland Australia have been colonised successfully by 20 species of freshwater fishes exotic to the continent, including 6 poeciliids, 3 salmonids, 4 cyprinids, 5 cichlids, 1 percid and 1 cobitid (Table 1). There are also populations of several exotic species living in outdoor ornamental ponds and artificially heated waters, as well as populations maintained by stocking, but these fishes are not considered to be truly feral because they are not self-maintaining (McKay 1989; Table 1).

A number of reviews have summarised the origins and distributions of introduced species in Australia, some of their effects on aquatic ecosystems, especially impacts on endemic fish species, as well as management and policy issues (Pollard et al. 1980; Tilzey 1980; McKay 1978; Arthington et al. 1983; McKay 1984; Arthington 1986; Arthington and Mitchell 1986; Fletcher 1986; Lloyd et al. 1986; Arthington and Lloyd 1989; Arthington 1989a; McKay 1989). The effects of translocating indigenous species between drainages have received less attention. McKay (1989) summarised and updated the relevant literature, giving a species by species account of known translocations and introductions in Australia. Reviews on these themes have most recently been published in the Proceedings of the Australian Society for Fish Biology's workshop on "Introduced and Translocated Fishes and their Ecological Effects" (Pollard 1990).

The objectives of this paper are to review the ecological and genetic consequences of species introductions, both planned and unintentional, to Australian waters. Emphasis is given to

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TABLE 1. Introduced freshwater fish that have established self-maintaining populations in Australian inland waters. S, sport fish; A, aquarium fish; B, biological control agent. Compiled from various sources, see Arthington (1986) and McKay (1989).

Family Species	Common name	Purpose of introduction
Salmonidae		
Salmo trutta L.	Brown trout	S
Oncorhynchus mykiss (Walbaum)	Rainbow trout	S
Salvelinus fontinalis (Mitchell)	Brook trout	S
Percidae		
Perca fluviatilis L.	European perch or redfin	S
Cyprinidae		
Cyprinus carpio L.	European carp	S
Carassius auratus L.	Goldfish	A
Tinca tinca (L.)	Tench	S
Rutilus rutilus (L.)	Roach	S
Poeciliidae		
Gambusia holbrooki	Mosquitofish	A/B
Xiphophorus helleri (Gunther)	Swordtail	A
Xiphophorus maculatus (Heckel)	Platy	A
Poecilia reticulata Peters	Guppy	A/B
Poecilia latipinna Le Sueur	Sailfin molly	A
Phalloceros caudimaculatus Hensel	One-spot live-bearer	A
Cichlidae		
Oreochromis mossambicus (Peters)	Mozambique mouth-brooder	A
Oreochromis sp.		A
Tilapia mariae Boulenger	Black mangrove or Niger cichlid	A
Cichlasoma nigrofasciatum (Gunther)	Convict cichlid	A
Cichlasoma octofasciatum (Regan)	Jack Dempsey cichlid	A
Cobitidae		
Misgurnus anguillicaudatus	Oriental weather loach	A

sub-tropical and tropical species, since they appear to present the greatest threat to natural ecosystems and are the subject of vigorous research and public education programs. Problems arising from the translocation of indigenous Australian fishes between drainage systems to supplement recreational fishing are noted but cannot be treated fully here. However, the case of the Lake Eacham rainbowfish (*Melanotaenia eachamensis*), supposedly brought close to extinction in its natural habitat by translocated Australian piscivores, is reviewed.

The final topic of the paper is the need for proper assessment of candidate species for introduction and translocation and the areas of theoretical ecology which may assist in predicting future impacts of introduced species.

Impacts of Introduced Fishes

The major impacts of introduced fishes may involve genetic effects, such as hybridization with indigenous fish species and between exotic species and strains, habitat and water quality alterations, competition for space and food, predation and the introduction of exotic parasites and diseases (Courtenay and Stauffer 1984; Moyle et al. 1986). Evidence of these impacts is reviewed for important representatives of the five fish families introduced into Australia, i.e. the Salmonidae, Percidae, Cyprinidae, Poeciliidae, Cichlidae and Cobitidae (Table 1).

Hybridization

Australia has not experienced the adverse impacts of hybridization seen in other countries because there are no indigenous representatives of the families that have been introduced. Hybridization has occurred between introduced European carp, *Cyprinus carpio* and goldfish, *Carassius auratus* (Hume et al. 1983) and between Atlantic salmon, *Salmo salar*, and brown trout, *S. trutta*, in hatcheries (Johnson, in Fletcher 1986). Of greater significance in Australia has been hybridization between two or possibly more imported varieties of the European carp, *Cyprinus carpio*, giving rise to the vigorous "Boolara" strain. Originally confined to south-eastern Victoria, this strain spread explosively throughout the Murray–Darling River system in the 1960's and early 1970's, becoming far more widespread and problematic than two other stocks which remained confined to the original sites of introduction, the Prospect Reservoir near Sydney and the Murrumbidgee Irrigation area of New South Wales (Shearer and Mulley 1978; Pollard et al. 1980; Fig. 2). The Boolara strain is believed to be a hybrid between an introduced mirror variety and a fully scaled carp variety of unknown origin. This parallels several cases of intraspecific hybridization among introduced plants, giving rise to locally adapted as well as aggressive variants (Barrett 1982).

The hybrid carp episode has stimulated comparable research on the introduced Mozambique tilapia, *Oreochromis mossambicus*, in Australia. This species has established feral populations in Queensland and Western Australia by several mechanisms, including escape of fish from outdoor ornamental ponds during flooding, disposal of aquarium fish into impoundments and riverine pools, and possibly also deliberate releases to enhance indigenous recreational fisheries. Electrophoretic analysis shows that populations of *O. mossambicus* in Brisbane

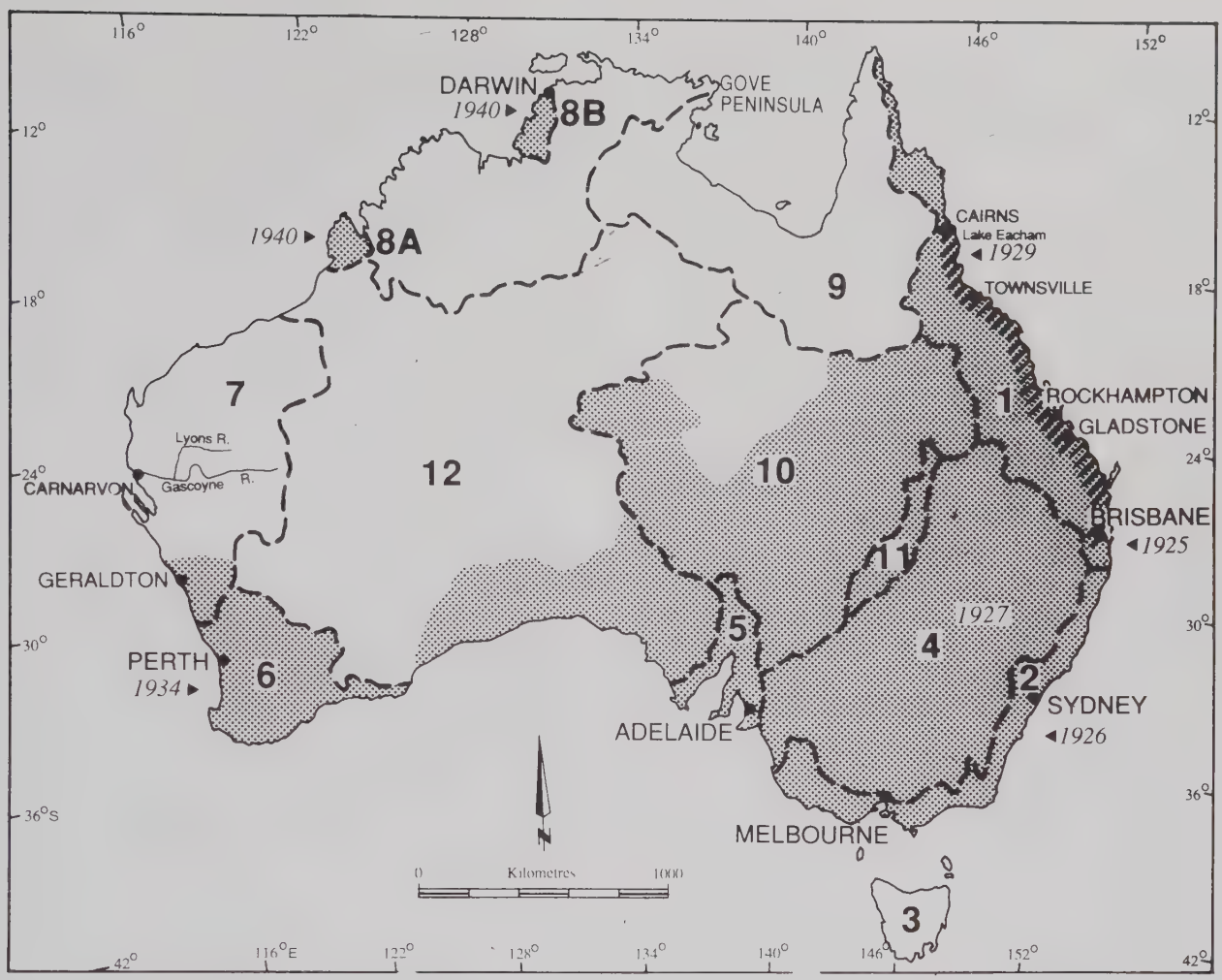

FIG. 1. Australia, showing major drainage divisions (see 1–12 below), the distribution of *G. holbrooki* (speckled areas) with dates of major introductions (e.g. Cairns 1929), the distribution of *Poecilia reticulata* (cross-hatched area), localities supporting *Oreochromis mossambicus* (Brisbane, Townsville, Cairns, Queensland; Gascoyne and Lyons Rivers, Western Australia) and the location of Lake Eacham on the Atherton Tableland, southwest of Cairns. Numbers 1–12 refer to the drainage divisions recognised by the Australian Water Resources Council. Speckled areas indicate the presence of *G. holbrooki* within at least parts of the drainage division (from Lloyd et al. 1986, modified and redrawn). 1. North-east Coast Division, 2. South-east Coast Division, 3. Tasmanian Division, 4. Murray–Darling Division, 5. South Australian Gulf Division, 6. South-west Coast Division, 7. Indian Ocean Division, 8. Timor Sea Division: A — Cape Levesque Coast, B — Finnis River, 9. Gulf of Carpentaria Division, 10. Lake Eyre Division, 11. Bulloo-Bancannia Division, 12. Western Plateau Division.

and Townsville, Queensland, and the Gascoyne River, Western Australia (Fig. 1), are virtually identical genetically and represent a relatively pure strain. These populations differ significantly from another population occurring in Cairns, Queensland. The Cairns fish appear to be hybrids between *O. mossambicus* and *O. hornorum*, and possibly also *O. niloticus* (Bluhdorn et al. 1990). The presence of at least one hybrid strain of this troublesome cichlid in Australia is of concern because its physiological tolerances, ecological characteristics and consequent potential for spread and adverse impacts are wholly unknown. Experiences with hybrid tilapias in other countries demonstrate the significance of this problem and there will always remain the possibility of further hybridization among Australian stocks of *O. mossambicus* in the event of population mixing. At present the wide geographic separation of self-maintaining populations makes this unlikely, but not impossible, since illegal translocations have occurred within Queensland and between Queensland and New South Wales irrespective of the official "noxious" status of this species.

All populations of the mosquitofish, *Gambusia,* examined in Australia have been identified as the species *G. holbrooki* (Girard) (Lloyd and Tomasov 1985; Lloyd 1990a). Thus there is no threat of hybridization between this species and *G. affinis*, with the attendant implications for future spread and consequent ecological impact of hybrid strains (e.g. Reznik 1981). However, marked morphological and genetic differences have been found among Australian populations of *G. holbrooki* (Tomasov 1981), and Trendall (1982) demonstrated substantial variation in life-history traits in four populations of *G. holbrooki* from Western Australia. Hybridization among phenotypically and genetically distinct strains of this species is possible and could have unexpected outcomes.

These examples highlight the need for research on the genetic attributes of founding populations of successful (and unsuccessful) introduced fishes and on the genetic changes which may accompany colonization (via founder effects, genetic drift, mutation and selection). The explosive spread of European carp in Australia is an outstanding example of the differential suc-

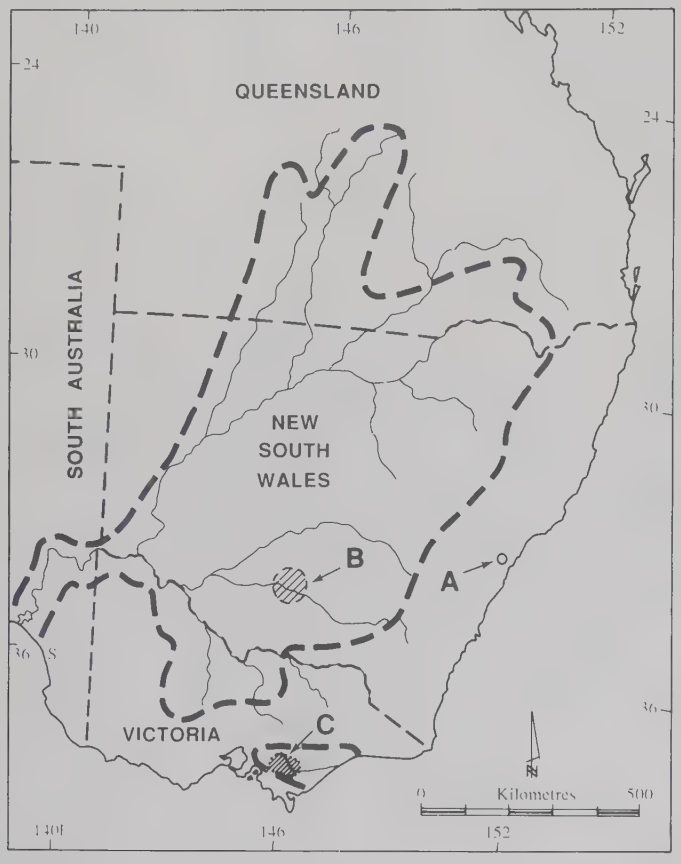

FIG. 2. States of Victoria and New South Wales, and parts of Queensland and South Australia, showing the distribution of three strains of European carp; A — Prospect Reservoir strain, B — Murrumbidgee Irrigation area strain, and C — the Boolara strain, which is now widespread throughout the area contained within the dotted lines.

cess of one genetic variant, and it is unfortunate that there is so little known about the relationships between genome, physiology and life history traits in the highly successful Boolara strain of carp and the two varieties which have remained so restricted in their distributions in Australia (Fig. 2). Although the range of the Boolara strain is still expanding and it achieves large local populations, it has declined in most areas from the peak population levels recorded at the height of the invasion (Morison and Hume 1990). This decline has been attributed to poor recruitment over several years, but Morison and Hume (1990) suggest that several good floods in the Murray–Darling system could reverse the trend.

Habitat Alterations

There is little evidence that introduced fishes have seriously altered aquatic habitats in Australia. European carp are often blamed for increased turbidity because they disturb bottom substrates during feeding but careful research in Australia has not substantiated this. Fletcher et al. (1985) concluded that populations of carp have not caused increased turbidity levels in the Lower Goulburn River Basin, Victoria; in this system turbidity increases were attributed largely to hydrologic changes during the study period. Any impact of carp on turbidity in Australian aquatic ecosystems seems to be obscured by the naturally high and variable turbidity of many inland waters (Kirk 1977) and the interaction of hydrological factors with soil type and land degradation. However, at very high densities in shallow, drying waterbodies, it is acknowledged that carp sometimes do cause increases in turbidity of the water (Fletcher et al. 1985).

It has been asserted that introduced carp populating many shallow lakes in North America cause increased turbidity, destroy beds of aquatic plants and by doing so destroy cover for juvenile fishes, as well as disturbing the complex substrates which produce invertebrate food organisms (Moyle et al. 1986). When carp are removed, turbidity decreases and native invertebrate-feeding fishes that locate their prey by sight increase (Taylor et al. 1984). Although the relationship between introduced carp and these environmental changes has not been rigorously documented, Moyle et al. (1986) maintain that the events described are so widespread in North America that other explanations are unlikely.

Australian research has indicated that *Potamogeton pectinatus*, a shallow rooted, soft-leaved species, may be the only aquatic plant reduced by carp in this country (Fletcher et al. 1985). Most of the aquatic plants affected by carp in the United States and France are also soft-leaved species, particularly species of *Potamogeton* and *Chara* (Crivelli 1983).

Turning to the Poeciliidae, *Xiphophorus helleri*, the swordtail, is predominantly herbivorous with a small component of aquatic invertebrates in its diet (Arthington 1989), but there is no clear evidence that its feeding has contributed to changes in aquatic macrophyte or algal communities. Rather, the loss of indigenous aquatic macrophytes from Brisbane's urban creeks has resulted from dredging, channel modifications, siltation, dumping of domestic and garden rubbish by riparian landowners, bank erosion and the invasion of introduced plants (Arthington et al. 1983). The control of water hyacinth (*Eichhornia crassipes*) and other introduced plants using herbicides may also have contributed to the decline of some indigenous macrophytes. Increased algal densities have resulted from the selective planktonic feeding of *Gambusia holbrooki* in experimental ponds (Hurlbert et al. 1972) but whether *Gambusia* has this effect in Australian and other waters is not known.

The diet of Mozambique tilapia has been investigated in a productive sub-tropical impoundment with dense littoral stands of *Hydrilla verticillata* and other submerged macrophytes. *Oreochromis mossambicus* derived 94% of its diet from *H. verticillata*, phytoplankton and filamentous algae, and this plant also constituted 34% of the diet of the indigenous spangled perch, *Leiopotherapon unicolor* (Bluhdorn et al. 1990). The high contribution of *H. verticillata* and algae to the diet of *O. mossambicus* reflects the true herbivory of this fish compared to the opportunistic omnivory of *L. unicolor*, yet it is probable that both fishes contribute to regulation of macrophyte biomass in this impoundment. *Oreochromis mossambicus* has been used in other countries to control aquatic weeds and algae in irrigation canals and rice fields (Erdman 1984; Shireman 1984), and in an integrated algae-mosquito control program where fish grazing reduced the filamentous algae sheltering mosquito larvae from predators. However, *O. mossambicus* cannot be used at present for biocontrol purposes because of its noxious status in Queensland and the illegality of stocking or translocating this fish between waterbodies (see Arthington 1986). Regrettably, this has not prevented illegal attempts to use this species to control algae in ornamental ponds receiving nutrient-rich runoff from a resort golf course, and to entertain visitors as a sideline. Species of tilapia have been introduced in various countries specifically to control aquatic plants, but *Tilapia zilli* reduced the abundance of macrophytes in Califor-

nian drainage systems to such a serious extent that its release for plant control was abandoned.

The case for such uses of *O. mossambicus* in Australia is frequently raised and eventually must be evaluated by management authorities. The use of fish in biological control should not be undertaken lightly, as world experience with *Gambusia* in mosquito control has amply demonstrated (Lloyd 1990a). Fish are rarely monophagous and even the essentially herbivorous/detrivorous tilapias are omnivorous as juveniles and may therefore have an impact on non-target organisms. The use of triploid grass carp, *Ctenopharyngodon idella*, for control of aquatic plants in ponds, lakes and impoundments (but not in flowing waters) may be one of the few successes in biological control using fish (Courtenay 1990; McDowall 1990).

Impacts of Competition on Indigenous Fishes

Resource competition for food, perhaps mediated by interference and aggression, seems to be one of the most probable mechanisms of impact of introduced species. Taylor et al. (1984) and Arthington and Mitchell (1986) point out that successful introduced fishes typically exhibit generalist feeding habits and trophic opportunism. There is consequently considerable overlap in the diets of introduced and indigenous fishes in many waterbodies. *Gambusia holbrooki* and Australian melanotaeniids, atherinids, galaxiids and a retropinnid have very similar diets (Lloyd 1987, 1990b; Arthington 1989b) and the diet of the rainbowfish, *Melanotaenia duboulayi* (Castelnau) seems to change when large numbers of mosquitofish and rainbowfish co-exist. Herbivory is more important, and terrestrial insects falling on the water's surface are less important, in the diet of the rainbowfish in these situations. Also *M. duboulayi* tends to select larger prey items in the presence of *G. holbrooki*, which actively selects very small prey from the invertebrates available in the stream environment. These shifts reduce dietary overlap between the two species, and may contribute to partitioning of food resources. However, it is not known how dietary niche shifts affect growth, reproduction and recruitment of this or any other species. Aggression, predation on eggs and fry and environmental disturbances causing loss of aquatic macrophytes required for rainbowfish spawning habitat may also be involved in the decline of this species in urban streams supporting poeciliids (Arthington et al. 1983; Milton and Arthington 1984).

There is other field and experimental evidence that Australian fishes display niche shifts in the presence of *G. holbrooki*. Lloyd (1987) recorded an expansion of niche width rather than a reduction as predicted by competition theory (O'Connor et al. 1975). As a corollory of dietary niche shifts in the presence of *G. holbrooki*, some indigenous fishes show shifts in distribution and abundance (Lloyd 1987; Lloyd 1990b). A mutually exclusive distribution pattern exists between the mosquitofish and the Pigmy perch, *Nannoperca australis*, in the lower River Murray (Lloyd 1984; Lloyd and Walker 1986). Other species, such as melanotaeniids, atherinids, galaxiids and a retropinnid, show much lower abundances in the presence of *G. holbrooki* and *X. helleri* than in habitats without introduced fishes (Arthington et al. 1983; Lloyd 1987). Some of these relationships have been documented mainly in disturbed systems where it is difficult to separate the influence of habitat disturbance and loss of heterogeneity from the effects of introduced fishes.

The one-spot live-bearer, *Phalloceros caudimaculatus*, and the guppy, *Poecilia reticulata*, have diets similar to that of the mosquitofish (Arthington 1989b) but are less aggressive species (Griffiths 1972). Their impacts on Australian endemic fishes have not been studied, although where guppies and *G. holbrooki* are abundant in disturbed Queensland creeks, endemic fishes tend to be rare (McKay 1978; Arthington et al. 1983).

The ecological impact of interference competition as a result of aggression and fin-nipping by *G. holbrooki* is thought to be important. Lloyd (1987, 1990) showed that mosquitofish will attack native fish twice their size and can inflict body scale and caudal fin damage; such fish are susceptible to disease. Schoenherr (1981) interpreted the aggressive behaviour of *G. holbrooki* towards gravid female Gila (Sonoran) topminnow, *Poeciliopsis occidentalis*, leading to the complete suppression of reproduction, as interspecific competition for space, but Meffe (1985) felt that while some interference occurs, predation by *G. holbrooki* has been more important in the decline of the Gila topminnow. McKay (1978, 1984) suggested that the sheer numbers of mosquitofish and swordtails in creeks could adversely affect indigenous fishes.

The decline of indigenous fishes in Australia and elsewhere has most often occurred in disturbed and polluted habitats which introduced species such as poeciliids, cyprinids and cichlids are able to exploit because of their broad environmental tolerances, flexible habitat requirements and trophic opportunism (Arthington et al. 1983; Courtenay and Stauffer 1984; Moyle et al. 1986; Arthington and Lloyd 1989; Arthington et al. 1990). In theoretical terms, the significance of habitat disturbance lies in the enhancement of the competitive ability of introduced species (Arthington et al. 1990), i.e. an increase in the alpha-coefficient of the introduced species and a decrease in the beta coefficient of the indigenous species (see Lotka-Volterra equations, Krebs 1978). A review of the association between exotic fishes and disturbed habitats in Australian waters elaborates this point (Arthington et al. 1990). Courtenay (1990) sums it up nicely with his concept of synergism between the perturbations caused by exotic fishes and habitat alterations.

Gambusia holbrooki and other poeciliids have also colonised undisturbed waterbodies in Australia (Lloyd 1987) and may have caused the decline of an indigenous rainbowfish, *Rhadinocentrus ornatus* (Regan), in the near pristine environment of a dystrophic sedge swamp on North Stradbroke Island, Queensland. Like *G. holbrooki*, this rainbowfish feeds predominantly on terrestrial insects at the water's surface and small aquatic invertebrates (Bayly et al. 1975), and this may therefore be a case of competitive displacement (Arthington 1984). However, predation on eggs and fry of the endemic species may also have been involved. The interactions between *G. holbrooki, R. ornatus* and two indigenous species with restricted distributions in dunal wetlands (the honey blue-eye, *Pseudomugil mellis*, and the Oxleyan pigmy perch, *Nannoperca oxleyana*) are curently being investigated.

The decline and fragmentation of range of the Australian galaxiid, *Galaxias olidus*, and the decline of river blackfish, *Gadopsis marmoratus*, may be due to exploitation competition with brown trout, since their diets are similar (Fletcher 1979; Jackson 1978). *Galaxias olidus* can be abundant above waterfalls that exclude trout but be rarer below them, a situation comparable to the distributions of common river galaxias, *G. vulgaris*, and trout in New Zealand streams (McDowall 1990). The diet of introduced carp overlaps at various body sizes with that of several indigenous fishes, such as bony bream, *Nematolosa erebi*, freshwater catfish, *Tandanus tandanus*, sil-

ver perch, *Bidyanus bidyanus*, Australian smelt, *Retropinna semoni*, carp gudgeon, *Hypseleotris klunzingeri*, and flat-headed galaxias, *Galaxias rostratus* (Fletcher 1986). Whether any of these species has been affected by exploitation competition is not known.

Impacts of Predation on Indigenous Fishes

Gambusia has earned the name "fish destroyer" by attacking the eggs and fry of important sport fishes (Myers 1965); it is also well known that mosquitofish may be piscivorous. Australian dietary studies on *G. holbrooki* have not produced any evidence of piscivory (Cadwallader 1979; Lloyd 1987; Arthington 1989b), possibly because standard methods of gut content analysis underestimate rapidly digested foods such as fish (Meffe 1985). Yet *G. holbrooki* attacks and eats fish fry in aquaria (Johnson 1976; Meffe 1985; Lloyd 1987). Meffe (1985) calculated that a single female mosquitofish could eat the entire annual production of fry of the Gila topminnow and concluded that even rare predation on fry could have a significant impact on a species with low fecundity. Several small-bodied native fishes evidently affected by the mosquitofish in Australia have low fecundity (Milton and Arthington 1983b, 1984, 1985) but others do not (Lloyd pers. comm.).

Fletcher (1986) suggested that introduced brown trout, chinook salmon and redfin may have affected the numbers of galaxiids, pigmy perch (*Nannoperca australis*) and golden perch (*Macquaria ambigua*) in southern rivers by feeding selectively on small endemic fishes and fish fry.

Impacts of Predation on Invertebrates

Several studies have demonstrated the destructive effects of *G. holbrooki* on invertebrate populations in various field situations (Stephanides 1964; Legner and Medved 1974) and in controlled experiments. Beetles (Walters and Legner 1980), back swimmers (Hurlbert and Mulla 1981), rotifers and crustaceans (Hurlbert et al. 1972) and molluscs (Rees 1979) have been affected. In a few situations, mosquitofish feeding has been turned to advantage in the control of mosquito populations but many biologists maintain that its role is relatively insignificant (for reviews see Lloyd 1986, 1990).

In Brisbane streams, *G. holbrooki* feeds on small terrestrial insects and immature stages of aquatic insects in the drift and amongst aquatic plants, actively selecting very small prey (Arthington 1989b). Such size selective feeding might affect the structure of invertebrate communities by altering recruitment of various taxa. However, the impacts of *G. holbrooki* and other insectivorous fishes on invertebrate communities have not been studied in Australia and certainly require attention.

The decline of the Tasmanian mountain shrimp, *Anaspides tasmaniae*, may have been caused by brown trout feeding, as may the elimination and reduction of several Plecoptera and Trichoptera in Victorian streams (Fletcher 1979). European carp have caused the decline of a species of *Daphnia* in experimental ponds (Fletcher 1986).

Introduction of Parasites and Diseases

Many biologists oppose the importation of exotic aquarium species partly because exotic diseases and parasites may be introduced together with them (see McKay 1984; Langdon 1990). There is certainly evidence that disease organisms have entered Australia via the aquarium trade. Langdon (1990) summarised the major pathogens of fish in Australia. The importation of Japanese goldfish infected with *Aeromonas salmonicida* to Victoria in the 1970's (Trust et al. 1980) brought goldfish ulcer disease to cultured and wild Australian goldfish and carp populations; recent studies have demonstrated the pathogenicity of this bacterium to salmonids (Whittington and Cullis, 1988). Langdon (1986) and Langdon et al. (1987) described a new viral disease, Epizootic Haematopoietic Necrosis Virus (EHNV), of unknown origin, affecting redfin, *Perca fluviatilis*, in the wild and which had spread to cultured rainbow trout in 1986. This disease is highly pathogenic to several indigenous Australian fishes, including silver perch, mountain galaxias and Macquarie perch; it also has a pathogenic effect on *Gambusia* (Langdon 1989).

Concern over imported fish diseases has led to the establishment of quarantine facilities at major ports handling aquarium stocks (McKay 1984) and some states have banned translocations of introduced fishes because of the threat of disease. Victoria has banned translocation of redfin and Tasmania now requires that imported goldfish be certified free of goldfish ulcer disease (Langdon 1990).

Fish introductions were responsible for importing fish parasites such as the fish louse, *Argulus* (Williams 1980), and anchor worm, *Lernaea cyprinacea* (Roberts 1978), now common in several indigenous Australian fishes. There are very few Australian records of parasitism in *G. holbrooki* even though the mosquitofish is host to 23 species of parasites in North America (Lloyd 1984, 1987); a species of *Lernaea* seems the most common, at least in the River Murray. Moyle (1985) noted that indigenous Californian fishes seemed to be more heavily parasitized by exotic parasites, such as *L. cyprinacea*, than exotic fishes. This has also been observed with diseases. Langdon (1990) reported several instances where infectious agents are more pathogenic, or only cause clinical disease, in atypical hosts, and so become a problem when the typical host species come into contact with unusual hosts. Examples are whirling disease in rainbow trout, proliferative kidney disease of salmonids and the North American crayfish plague fungus which has devastated European astacids.

Overview of Impacts of Introduced Fishes

The exotic species of most immediate concern in Australia are aquarium species established in sub-tropical and tropical areas, particularly *G. holbrooki, X. helleri, P. reticulata, O. mossambicus* and *Tilapia mariae*. Salmonids have been present in temperate Australia for approximately 100 years and are highly prized for sport fishing. However, ecological impacts of salmonids, cyprinids and the European perch (redfin) are becoming evident in Australia (Pollard et al. 1980; Tilzey 1980; Fletcher 1986; Burchmore and Battaglene 1990) and there is a considerable research effort on management issues, including the genetic effects of multiple stocking programs.

Gambusia holbrooki has become a very common species in a wide variety of inland waters in 10 Australian drainage systems (Fig. 1). Large populations occur in habitats ranging from almost completely undisturbed, dystrophic swamps and streams, and freshwater and saline lakes, to polluted urban drains with a variety of water quality problems. *Gambusia holbrooki* is not considered to perform any useful ecological roles in Australian waters and although it may form part of the diet of water birds and indigenous piscivores, it is avoided by other fish when there is a choice of food (Lloyd 1987). *Gambusia*

holbrooki is also considered to be less useful as an agent in mosquito control than various indigenous insectivorous fishes (Lloyd 1986, 1990a; Arthington and Lloyd 1989). Several studies suggest that this species is partly responsible for the decline of small-bodied indigenous fishes, including species which play an important part in mosquito control (Arthington et al. 1983; Lloyd 1984, 1986; Lloyd et al. 1986; McKay 1978, 1984). The general view is that *G. holbrooki* is a pest or ecological "weed" (Lloyd 1984; Lloyd et al. 1986; Arthington and Lloyd 1989).

Xiphophorus helleri is also quite common in and around Brisbane, Queensland, and in coastal streams further north, but its ecological impacts have not been investigated. Its persistence and proliferation since introduction are of concern, particularly since it often occurs together with *G. holbrooki* and the two species together in large numbers seem to stress indigenous fishes (McKay 1978; Arthington et al. 1983). *Poecilia reticulata*, like the mosquitofish, was spread for mosquito control, and now occurs in many Queensland coastal streams (Fig. 1). It has a similar diet to *G. holbrooki* and where the two species are abundant in Brisbane creeks, some indigenous fishes are rare (McKay 1978; Arthington et al. 1983). *Poecilia latipinna*, *X. maculatus* and *Phalloceros caudimaculatus* are patchily distributed in Australia, but in sub-tropical and tropical areas these species could spread and have adverse effects (McKay 1978; Balla et al. 1985). The most recent aquarium fish to establish in Australia is the Oriental weather loach, *Misgurnus anguillicaudatus*, first found in the Yarra River, Victoria, in 1984 (Allen 1984); it now inhabits about 25 km of local streams around Canberra in the Australian Capital Territory. Other populations of this fish have been recorded in a river south-west of Sydney, New South Wales, and at three localities in Victoria (Lintermans et al. 1990; Burchmore et al. 1990). Environmental tolerances of the weather loach closely match those of *G. holbrooki* and they can also move across land so are effective colonisers. Ecological effects are presently unknown.

The cichlid *O. mossambicus* is probably the species of greatest current concern, given its adaptability and poor record in many other countries. It now occurs around Brisbane, Townsville, Cairns and in Western Australia, and new populations are being documented along the Queensland coast, especially north of Townsville and Cairns (Fig. 1). The current policy is to eradicate the smaller, more accessible populations, but the species appears to be spreading naturally, at least locally. For instance, many mature fish were carried over the spillway of North Pine Dam, Brisbane, during a recent period of flooding, and may have colonized (or recolonized) the downstream reaches of the North Pine River. In Townsville, *O. mossambicus* is abundant in urban drains connected to natural freshwater and tidal waterways. It occurs in tidal areas near Cairns and there is general concern that its ability to reproduce in sea water (Hora and Pillay 1962) may permit it to spread to new river systems via estuaries and coastal waters, although estuarine currents and predators may limit this to some extent (Whitfield and Blaber 1979). *Oreochromis mossambicus* has been declared a noxious species in northern Australia and in New South Wales, with very heavy penalties for translocation and cultivation (see Arthington 1986), but it has nevertheless turned up in isolated farm dams and outdoor ornamental ponds where its presence can only be attributed to human intervention. The populations recorded in Western Australia appear at present to be restricted to one drainage system in a semi-arid zone, but have definitely spread naturally, moving inland along drainage lines under the harsh environmental conditions imposed by seasonal flooding and droughts (Bluhdorn et al. 1990). In this environment, and in a tidal habitat near Cairns, significant stunting has occurred, evidently in response to environmental stresses (Bluhdorn and Arthington 1990a).

The distribution, population genetics, ecology and impact of *O. mossambicus* in Australia have been the subject of an intensive research program at Griffith University (see Arthington and Milton 1986; Bluhdorn et al. 1990; Bluhdorn and Arthington 1990a, b), but many important issues remain to be investigated before it will be possible to understand the process of invasion by this species, or how best to approach its management.

The Lake Eacham Rainbowfish

The Lake Eacham rainbowfish, *Melanotaenia eachamensis*, Allen and Cross, is endemic to Lake Eacham, a crater lake situated in a tropical rainforest catchment on the Atherton Tableland, near Cairns, northern Queensland (Fig. 1). The rainbowfish and two other indigenous fishes both widespread in northern Queensland, were abundant in the lake before 1984 (Allen and Cross 1982; McKay 1987), but during the mid-1980's, McKay and others noted the decline of the rainbowfish and the appearance of four additional fish species indigenous to the region around Lake Eacham but not previously recorded in the lake itself (it being in a closed catchment). These fishes included a mouth-brooding apogonid, the mouth almighty, *Glossamia aprion* (Richardson), the archer fish, *Toxotes chatareus* (Hamilton), the body bream *Nematolosa erebi* (Gunther) and the banded grunter, *Amniataba percoides* (Gunther).

Translocations of fishes between drainage systems have occurred many times in northern Queensland since the 1950's (as documented by local fishing clubs), but the translocations into Lake Eacham have not been recorded and were certainly unauthorised. The rainbowfish subsequently declined rapidly and in early 1987 Barlow and colleagues found only the four translocated species, and one of the original endemics, the hardyhead, *Craterocephalus stercusmuscarum* (Gunther); the Lake Eacham rainbowfish was not even sighted during these surveys. Barlow et al. (1987) presented circumstantial evidence that its extinction may have been due largely to predation by the carnivorous mouth almighty and possibly also the archer fish; two other indigenous fish species and a crayfish also declined in the lake after the translocations.

The Lake Eacham rainbowfish became somewhat of a "cause celebre" with aquarists and members of the Australia New Guinea Fishes Association (ANGFA). Aquarium specimens which had been gathered previously became the progenitors of pond-breeding populations, with the intention of restocking Lake Eacham and other suitable waterbodies nearby. However, there has been no resolution to the problem of how to clear Lake Eacham of its translocated piscivores. McKay (pers. comm.) suggested that the introduction of a voracious predatory fish might achieve sufficient population depression (or even full eradication) to warrant restocking with the rainbowfish. He nominated the indigenous silver barramundi, *Lates calcarifer* Bloch, since it is unable to breed in closed lakes and could in theory be completely eliminated after extirpation of all translocated fishes, either by allowing the introduced stocks to die out, or by concerted fishing efforts. The barramundi is a very popular recreational species in Queensland, so it may be possible to achieve its eradication from Lake Eacham by

encouraging local anglers and angling competitions. However, Lake Eacham is the focal point of Lake Eacham National Park, and it seems unlikely that the introduction of barramundi will be permitted by the authorities, given the problems caused by translocated piscivores in general and the improbability of achieving complete eradication of any species in a large, deep lake.

The stocking of nearby waterbodies with Lake Eacham rainbowfish presents other problems. Most contain another indigenous rainbowfish, *Melanotaenia splendida*, but there is evidence from electrophoretic studies of recent gene exchange between *M. eachamensis* and *M. splendida* (Dr Walter Ivanstoff, Macquarie University, pers. comm.). The specific status accorded the Lake Eacham rainbowfish may now be open to question.

M. splendida is very widespread in northern Queensland, existing as several colour morphs (Arthington and Wager, unpublished data), some evidently able to coexist in streams and riverine pools with the piscivores translocated into Lake Eacham and with other species. If the Lake Eacham rainbowfish is merely another morph of *M. splendida*, why has it fared so poorly in the presence of translocated piscivores with which other forms of this species are able to coexist elsewhere in the region? The answer may lie in unexplored aspects of predator–prey relationships, coupled with the influence of the particular environmental features of Lake Eacham; one feature may be the very high clarity of the water and hence the visibility of the rainbowfish to piscivores.

Can We Predict Future Trends?

Successful introduced fishes may experience local genetic differentiation following invasion of new environments (Arthington and Mitchell 1986). Whether this occurs will depend on the features of environments encountered, the range and distribution of genetic variation available to populations, and the inheritance patterns of traits conferring increased fitness (Barrett and Richardson 1986).

There are several examples of adaptive changes in fish following colonization events. The mosquitofish exists as both warm-adapted and cold-adapted strains in the USA (Otto 1973), and a Western Australian population of rainbow trout, *Oncorhynchus mykiss*, exists with higher summer temperature tolerance than its eastern counterparts (Morrissy 1973). The rainbow trout in New Zealand has superior swimming speed compared to stocks from the United States (Tsuyuki and Williscroft 1977). Tomasov (1981) showed that there are both morphological and electrophoretic differences between many Australian populations of *G. holbrooki*, and Congdon (pers. comm.) has established that genetic divergence between two riverine mosquitofish populations can be attributed to natural selection associated with hypersaline conditions caused by tidal inundation in the lower river reaches.

Shifts in thermal tolerance might be expected in *G. holbrooki* populations from southern and northern Australia, where temperature regimes are very different. Likewise, *X. helleri* and *O. mossambicus* may be undergoing selection for cold tolerance in Brisbane, where low winter temperatures have intermittently caused large fish kills in streams and impoundments (McKay 1978, 1984). Several male *O. mossambicus* kept in a small outdoor pond in Brisbane survived winter temperatures of less than 10°C (personal observation).

Shifts in critical physiological tolerances, particularly thermal minima, suggest that the future range of an introduced species cannot be predicted with certainty. Appreciation of this and other problems has led Australian fisheries authorities to restrict the introduction of certain aquarium species (although many species are still introduced annually) and to reject the idea of introducing the Nile perch, *Lates niloticus*, to stock northern waterbodies for recreational fishing (Barlow and Lisle 1987; Barlow and Rodgers 1990). In part, the case made against the introduction of Nile perch was that it could colonize the upper reaches of the Murray–Darling River system (Fig. 2) and affect important indigenous fishes which are recruited from these waters. A similar argument could apply to tilapia. Mature *O. mossambicus* die at temperatures ranging from 5 to 14°C (Mar et al. 1966; Kirk 1972). In suitable habitats this species may also survive winter temperatures in the upper Murray–Darling River system (see data in Barlow and Lisle 1987) although its spread further south would be temperature limited.

An Ecological Approach to Predicting the Outcome of Fish Introductions

There is worldwide evidence that successful fish introductions alter the structure and species composition of the invaded community and that most instances of introductions worldwide have had few direct benefits to society (Welcomme 1988; Courtenay 1990). Australian examples of impacts are accumulating with increasing research effort and the elapse of time following initial introductions. The demand for predictive capability with respect to potential impacts is as fervent in Australia as elsewhere, especially among members of the aquarium and aquaculture trades. A better understanding of the ecology of biological invasions is clearly required. Arthington and Mitchell (1986) presented a simple model of the invasive process as it may apply to fish. Herbold and Moyle (1986) and Moyle et al. (1986) have argued that introduced species do not fill 'vacant niches' as Simberloff (1981) concluded from his review of species introductions. Rather, they fit into the new environment by further compressing the 'realised niche' of one or more of the species already present, often to the point where the environment can no longer support the indigenous species (Moyle et al. 1986). In disturbed environments especially, introduced species may have a competitive advantage over the indigenous fish fauna (see Arthington et al. 1990; Courtenay et al. 1974).

Drawing upon the experience of entomologists in the biological control of pest species, Li and Moyle (1981) suggest four criteria for fish species that are candidates for introduction: trophic co-adaptation with members of the assemblage receiving the introduced species; narrow niche breadth including stenophagy; low vagility; and freedom from contagious diseases and parasites exotic to the new environment. These criteria are the antithesis of the typical characteristics of successful and troublesome introduced fish species around the world, i.e. zero or little trophic co-adaptation, broad niches, high vagility and the probability that they may carry exotic parasites and diseases (see Arthington and Mitchell 1986).

Moyle et al. (1986) suggested three areas of ecological theory that are particularly relevant to predicting the effects of introduced species. The theory of island biogeography may contriubte to consideration of the question "how many species can an aquatic ecosystem support?"; the concept of "limiting similarity" may aid in predicting how morphologically similar species can co-exist in a community; and the analysis of food

webs may be useful for understanding the trophic interactions of introduced and indigenous species. Moyle et al. (1986) concluded that although each theoretical approach has weaknesses, they all point to the creation of inherently unstable fish communities through poorly considered introductions and translocations. The significance of habitat disturbance for the establishment of invading species also requires consideration (see Arthington et al. 1990).

Conclusions

Fisheries scientists and managers now have access to a substantial body of theoretical and empirical evidence that additions to indigenous fish faunas are seldom entirely successful and more often than not have unanticipated and undesirable consequences (Welcomme 1984, 1988; Courtenay 1990b; Arthington and Lloyd 1989). It is widely agreed that fish introductions should be preceded in every instance by full consideration of the probable consequences for the receiving aquatic ecosystem and its indigenous fish fauna, following the model of emtomologists working with entomophagous and parasitic insects introduced for biological control. This applies equally to the translocation of fishes between drainage systems, and is of particular concern in Australia at present because of the renewed interest in stocking inland waters to enhance recreational fishing (see Barlow et al. 1987; Harris and Battaglene 1990). The example of the impact of translocated piscivores on the Lake Eacham rainbowfish may not seem to be of great ecological consequence except as a conservation issue, but it serves the purpose of demonstrating that translocations of indigenous species have the potential to be as damaging as the introduction of exotic species.

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A North American Perspective

Introduced Freshwater Fishes: A Review of the North American Perspective With Emphasis on Canada[1]

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Crossman, E. J. 1991. Introduced freshwater fishes: a review of the North American perspective with emphasis on Canada. Can. J. Fish. Aquat. Sci. 48 (Suppl. 1): 46–57.

The introduction of fishes into North America began in the late 1600's. The number of species has increased over the years, with pulses in the late 1800's and following the 1950's. By 1989, there were 45 established exotic fishes in the continental USA, and 16 in Canada. By 1989, the number brought into, invading, or transferred within Canada was 92 species plus 13 subspecies and hybrids. A special situation for Canada is the steady invasion from U.S. waters. Over the years, 38 such species have been identified. A variety of societal pressures led to the introductions, and the species introduced represent a number of realized or potential environmental impacts. Various international, national, state and provincial agencies or programmes have developed to investigate introductions and/or judge individual applications for the importation or transfer of live fishes. The number and nature of species being moved is still not well known. For Canada, 125 forms (species, hybrids, selected strains) which fit the new definition of Introduced are summarized by province and mode of introduction.

L'introduction de poissons en Amérique du Nord a commencé à la fin du XVIIe siècle. Le nombre d'espèces a augmenté au cours des années, avec des bonds à la fin du XIXe siècle et après les années 1950. En 1989, il y avait 45 espèces de poissons exotiques établies dans les États-Unis continentaux et 16 au Canada. En 1989, le nombre d'espèces importées ou transférées au Canada, ou encore pénétrant d'elles-mêmes au Canada, était de 92, plus 13 sous-espèces ou hybrides. Ce qui est propre au Canada, c'est l'invasion par des poissons provenant des eaux américaines. Au cours des années, 38 espèces sont ainsi entrées chez nous. Diverses pressions sociales sont à l'origine de l'introduction d'une variété d'espèces, avec des conséquences environnementales prouvées ou potentielles certaines. Des organismes ou des programmes internationaux, nationaux ou provinciaux ont été mis sur pied pour étudier les introductions et juger des demandes d'importation ou de transfert de poissons vivants. Le nombre et la nature des espèces transportées ne sont pas encore bien connus. Pour le Canada, on a répertorié 125 formes (espèces, hybrides, souches sélectionnées) qui entrent dans la définition des espèces introduites, par province et par mode d'introduction.

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The history of the introduction of fishes into North America begins virtually with the arrival on the continent of Europeans. The earliest record of a fish species introduced into North America is usually given as that for the goldfish, *Carassius auratus*, in the late 1600's (DeKay 1842). After the middle of the 19th century there was a slow but steady increase in the number of fishes brought from foreign lands. Courtenay and Hensley (1980) plotted the change over time of the most critical group, those foreign species which became established (developed reproducing populations). Major periods of introductions of foreign species occurred in the late 1800's, and following the 1950's. The second, and greater increase led to an eventual figure of 35 exotics established in North America by 1980. By this date there were an additional 68 species in 20 families known to have been introduced into, or collected in, North American waters north of the Rio Grande River. Although a considerable number of these were tropical aquarium species limited to the southern U.S., they included a significant number of food and recreational species in both the U.S. and Canada.

By 1984, the number of established exotics in continental USA alone had grown to 41, and an additional 63 exotics were listed (Courtenay et al. 1984) for the same area as known but not established at that time. A further 168 species (Courtenay and Taylor 1984) had been transferred from one ecosystem to another within that area. By 1989 (Courtenay 1990) established exotics in the continental United States had increased to 45, there were 15 exotics which had been established and failed or were eradicated, and 56+ exotics were reported but not known to be established.

According to McCann (1984), there are over 2 000 exotic species (largely aquarium fishes) that have been imported into the U.S., or are likely to be imported in the near future. Courtenay (1990) quoted two authors, Ramsey and Boozer, as indicating that in the late 1970's and early 1980's nearly 200 million individuals of exotic fishes were imported annually into the U.S. and that this represents only 20% of the annual U.S. aquarium market. The rest is made up of exotics cultured in the U.S.

In Canada, there were five established exotics in 1955 (Mail 1954; Dymond 1955). By 1984, the number introduced had increased to 18 (Crossman 1984), but the number of species

[1]This paper forms part of the Proceedings of the Ecological and Genetic Implications of Fish Introductions Symposium (FIN) convened at the Great Lakes Institute, University of Windsor, Ontario, Canada, May 17–19, 1990.

established had risen only to nine. Canada has another phenomenon to contend with — the natural immigration of approximately 38 "Invasive Species" (cf. Hocutt 1985). These have moved into some part of Canada from the USA. They have moved from a foreign country, with or without man's assistance and would, threfore, qualify as exotic species by the definition used by the American Fisheries Society (AFS) in the past. The history of the introduction of 37 species of fishes into the Great Lakes is documented in papers providing faunal lists specific to one lake (e.g., Crossman and Van Meter 1979), and summarized for all lakes by Bailey and Smith (1981), Emery (1985), and Underhill (1986). Emery included several Canadian and U.S. records missed by others, and used a very broad concept for introduction.

Detailed distribution notes for exotic species are available for North America (Courtenay and Hensley 1980; Lee et al. 1980; Courtenay et al. 1986; Hocutt and Wiley 1986), continental USA (Courtenay et al. 1984), and Canada (Crossman 1984). The most recent edition of the AFS "List of Common and Scientific Names of Fishes from the United States and Canada" (Robins et al. 1991) includes, as an appendix, a section entitled "Exotic Fishes" (Courtenay et al. 1991).

Throughout this paper, common and scientific names, and the taxonomic order of families in the tables follow that given in the 1991 edition of the AFS Names List (Robins et al. 1991). There are many changes from those in previous lists.

It is virtually impossible to close the list of introduced fishes at any time. Since a 1989 list was prepared (Courtenay 1990), a circulated update (March 1989) listed the arrival in or increased distribution in, the U.S. of five exotic species or varieties. These included Austrian Seeforellen, *Salmo trutta,* introduced in New York, *Serrasalmus natteri*, captured in Alabama, and *Colossoma* sp. and *C. macropomum*, taken in Florida. Other reports include the establishment in the U.S. of the ruffe, *Gymnocephalus cernuus* and the bighead carp, *Hypothalmichthys nobilis*. The rudd, *Scardinius erythropthalmus*, has become established in the St. Lawrence River and has reached Canadian waters. The tubenose goby, *Proterorhinus marmoratus*, and the round goby, *Neogobius melanostomus*, have been captured in the St. Clair River (Crossman et al. 1992). The skipjack herring, *Alosa chrysochloris*, has been taken in Green Bay, Lake Michigan.

The human pressures to which intentional introductions, authorized and unauthorized, are usually attributed include the desire for new food and recreational fishes, the search for foreign species more tolerant of degraded environmental conditions, to fill perceived "vacant niches" in specific aquatic communities, simple nostalgia for familiar creatures from past homelands, constantly increasing numbers of new species for hobby aquarists, the release of hobby aquarium specimens when they get too large for tanks, foreign species for education and entertainment in public and commercial aquariums, species for cage culture as food which are sometimes genetically adjusted for better success, escape from such facilities, growing demand for bait fish, the captive rearing of them, and the transboundary transport of such species, and biological control of plants or other animals. To these must be added the very important but unintentional transfers such as in ships' ballast water.

Impact of Introduced Species

Magnuson (1976) invoked the Equilibrium Theory of Island Biogeography in a consideration of the impact on species dynamics in lakes of the introduction of new or exotic species.

The impact of introduced aquatic organisms on aquatic communities in the continental U.S. was summarized by Taylor et al. (1984). Kohler and Courtenay (1986b) classified negative impacts into five broad categories: habitat alteration, trophic alterations, spatial alterations, gene pool deterioration, and introduction of diseases. It is possible that introduced fishes may have operated in each of these.

Many authors have commented on the difficulty of documenting the specific role of introduced fishes in even obvious cases of depletions of native species. Hartman (1988), speaking of changes in the Great Lakes, remarked "the exotics that have invaded or been accidentally or purposefully released into the Great Lakes system have not only adversely affected indigenous fishes, but some have developed into new and valuable resources. However, when it comes to degradation of water quality and of critical habitat, the linkages to changes in fish populations are neither clear-cut nor quantifiable — their impacts were generally far more subtle and difficult to detect, but not necessarily of less importance."

An international symposium called "SCOL — Salmonid Communities in Oligotrophic Lakes" took place in 1971. The main goal was to attempt to identify the separate and joint effects of three major stresses imposed on fish communities by man: exploitation, cultural eutrophication, and species introduction (Stevenson 1972).

Miller et al. (1989), discussing extinction of North American fishes listed introduced species as a factor which at least contributed to the extinction of 27 of the 40 species discussed.

Authorized introductions are made with the intent of some beneficial impact. However, Regier (1968) warned that we choose exotics on the basis of what they can do for us and not primarily what they can do for the non-human system. We are all aware of the generally good impact of some introduced fishes. That of the rainbow trout, *Oncorhynchus mykiss*, when introduced into eastern North America is a good example. The introduction of the sea lamprey, *Petromyzon marinus*, into the upper Great Lakes must, I think, be one with a totally negative impact. At best, many are a mixed blessing.

Common carp, *Cyprinus carpio*, were introduced into Ontario in the late 1890's as a means of "furnishing in the future a cheap article of food." However, within 19 years, it was said that "it is generally conceded that the promiscuous introduction of carp on this continent has been attended with nothing but evil results" (Crossman 1968).

The white perch, *Morone americana*, invaded Lake Ontario around 1950 via the Erie Barge Canal and the Mohawk River. They were first seen in Lake Erie in 1953 and were firmly established by 1975 (Emery 1985). The potential impact of this introduced species on the indigenous yellow perch, *Perca flavescens*, in Lake Erie, has always been a concern. Hayward and Margraf (1987) indicated that the Lake Erie population of white perch expanded sharply in 1979 and said that the expanding population "may have exacerbated the food limitation for yellow perch" which began as one of the results of eutrophication. An introduced species was amplifying another man-made impact on an indigenous species.

The story of the rainbow smelt, *Osmerus mordax*, in the Great Lakes is reminiscent of the problem solving steps in the nonsense story about the lady who swallowed a fly. The Atlantic salmon, *Salmo salar*, was introduced in an inland lake in Michigan, a non-indigenous food fish, the rainbow smelt, was stocked with it. The desired introduced species failed to survive but the food species did and spread throughout the upper Great

Lakes as a result. As it expanded and increased, it was considered to have had an adverse impact on several commercially important whitefishes, *Coregonus* spp., and possibly contributed to the demise of the blue pike, *Stizostedion vitreum glaucum*. Later, Pacific salmon, *Oncorhynchus* spp. were introduced. This introduction was justified on the basis of providing new recreational species, and possibly in hopes of them utilizing the over-abundance of the alewife, *Alosa pseudoharengus*.

After invading Lake Simcoe, the smelt began to have a negative effect on the young of the lake whitefish, *Coregonus clupeaformis*, but became a major food source for lake trout, *Salvelinus namaycush*, and large yellow perch, *Perca flavescens*.

There are perennial complaints about the deterioration of angling success in the Kawartha Lakes of Ontario. If this concern has a biological basis, it is possible that the problem is, at least in part, an impact of the introduction into that somewhat unique ecosystem of a top-level, piscivorous predator, the walleye, *Stizostedion vitreum vitreum*, which did not occur there previously. The numbers of the indigenous cisco, *Coregonus artedi*, were noted to decline after that introduction.

There has been an increasing concern for the possible effect of loss of genetic fitness as a potential impact of introductions (Hocutt 1984; Smith 1985; Ferguson 1989). Recent information suggests that muskellunge, *Esox masquinongy*, when syntopic with northern pike, *E. lucius*, demonstrate reproductive adaptations (?) not possessed by allotopic populations. The only present source of fish culture support in Ontario uses gametes from an allotopic population. The use of this stock in syntopic habitats may be detrimental. Larkin (1981) challenged this attitude in regard to Pacific salmon. Gausen and Moen (1991) indicated that in Norway, the number of escaped farmed Atlantic salmon, *Salmo salar*, migrating into coastal waters each year was thought to be significantly greater than the number of wild salmon doing so. Escaped farmed salmon have major variations in biology and behaviour, and cross-breeding with wild salmon may lead to loss of genetically determined characteristics of local adaptive value to wild populations. Those authors cited the work of others indicating poorer performance of farmed fish.

Canadian freshwater habitats are usually considered cooler, and many fish faunas coldwater-adapted, relative to those in the U.S. As such, they are more vulnerable to the impact of climatic warming. This impact could be direct, as increased habitat temperatures, and indirect, as increased rate of invasion of southern fishes (Meisner et al. 1989; Mandrak 1988).

History of Concern and Problem of Terminology

One of the major difficulties in summarizing or enumerating fishes "introduced" into North America is the variation in emphasis and terminology that has been used by different authors. Until recently, the major concern has been for "exotic" fishes defined as derived from and native to, a foreign country. Although the concept of transplanted fishes, species native to North America and moved from one watershed to another within North America, was recognized and tabulated, this group was treated with far less concern. Often consideration was given only to those exotics which survive as naturally reproducing populations, using terms such as "established" or "naturally surviving." The numbers provided for a single area by different authors do not always agree.

Increased concern for introduced fishes began in the late 1960's. The 1968 annual meeting of the Canadian Committee on Freshwater Fisheries Research included "A symposium on introductions of exotic species" (Loftus 1968). At that conference, Regier (1968) used exotic to mean any species not native to the community under consideration.

In 1969, the American Fisheries Society (AFS) and the American Society of Ichthyologists and Herpetologists (ASIH) co-sponsored an "Invitational Conference on Exotic Fishes and Related Problems" (Lachner et al. 1970). The attempt to standardize terminology began at this time. A 1973 position statement by AFS suggested that species not native to an ecosystem will be termed exotic but the "foreign" element was still inherent in this concept. Hubbs (1977) defined an exotic species as one introduced to a location outside its natural geographic range. He included extracontinental and intracontinental introductions. Hubbs also suggested that long distance intracontinental introductions, especially those which cross major drainage barriers, may be equivalent to extracontinental introductions in impact. An Exotic Fish Section of the AFS was formed in 1980. Early publications which called attention to this continental concern were those of Courtenay and Robins (1973, 1975), Courtenay (1979) and Courtenay and Hensley (1979, 1980). Although some of these papers emphasized the situation in Florida, they were of continental significance in that Florida has been the "port of disembarkation" for many exotic species, and the centre of artificial culture from which others spread elsewhere in North America. Magnuson (1976) used the term exotic for new species from another continent or from an adjacent lake.

These papers were followed by the "Exotic Fish Symposium" at the AFS meeting in 1981. Again, the major emphasis was limited to the foreign concept of exotic species, both in the symposium and the resulting publication (Courtenay and Stauffer 1984). However, in that publication, Hocutt (1984) indicated that most U.S. states were using the broader Hubbs concept of exotic. The 1984 publication resulted in further discussions of terminology. Shafland and Lewis (1984) recommended terminology which proposed "Introduced" as the general term for organisms moved by man, "Exotic" as equal to foreign, and "Transplanted" as moved outside its natural range within a country where it occurs naturally. Hocutt (1985) responded with an alternative set of what he called biologically rather than politically based terms. These included the Hubbs concept for "Exotic," "Alien" meaning belonging to another place, or foreign, "Foreign" implying from a different biogeographical region, continent or subcontinent, and "Introduced" for deliberately or inadvertently transferred by man to an area outside its native range. Important from Canada's standpoint, Hocutt included a term "Invasive," meaning species which expand their range either as a consequence of a natural phenomenon or as a result of man's deliberate or inadvertent action.

The result of all this was the decision by AFS to establish the term "introduced" with the broader concern for all species moved into any habitat other than their original one.

For the consideration of introductions on a faunistic basis, even the definition of North America had to be examined. For most considerations, North America includes all of Mexico. Hocutt (1984) reiterated that faunistically, Mexico is a transition zone (between Nearctic and Neotropical) and that the definition of North America proposed by Miller and Smith (1986) was more appropriate. That definition provides for fishes a

southern boundary for North America extending into Mexico to 20°N on the Atlantic slope and just below 17°N on the Pacific slope. This corresponds to the southern limit of Cyprinidae. If we include the whole of Mexico, we must include the 1984 Mexican records of 55 exotic fishes of which 26 were of foreign origin and 29 were transplants (Contreras and Escalante 1984).

The various actions taken by AFS over the years have become referred to as a series of initiatives and were summarized by Kohler and Courtenay (1986a). These initiatives often included a summary of knowledge of introduced fishes, draft protocols for regulation of introductions, and strategies for studying species (see Kohler and Stanley 1984), and their potential impact on the recipient environment, prior to approval for introduction. The AFS Exotic Fish Section (changed to Introduced Fish Section in 1985) sponsored, in 1984, a special session entitled "Strategies for Reducing Risks from the Introduction of Aquatic Organisms." The goal of the session was said (Kohler 1986) to be "to put forth a message to concerned, and more important, by the concerned members of the fishery profession, as follows: (1) there are definite risks associated with the introduction of aquatic organisms; and (2) those risks, once recognized, can often be circumvented while still meeting the desired objectives... ." The major topics presented at the session had as a central theme strategies for reducing risks, not eliminating introductions. Those papers appeared in Fisheries 1986, 11(2). The cover title for that issue was "The Good, the Bad, and the Ugly: Introduced fishes." The standard terminology chosen for all papers in that series, and adopted for use by AFS, was that of Shafland and Lewis (1984), combining the concepts of exotics, transplants, and man's involvement in the term "Introduced." By implication, the term "Invasive" was split to exclude those that invaded as a result of man's involvement (e.g., watershed connections, canals, etc.). In the same set of papers, the 1972 "Position of the AFS on Introductions of Exotic Species" was modified (Kohler and Courtenay 1986b) by changing the operative term from "Exotic" to "Introduced" (= species not native to an ecosystem). From this point on in this paper, this most recent AFS concept of introduced will be used.

This useful and appropriate standardization does, however, complicate the task of compiling lists of introduced fishes. As a result, regardless of whether the sea lamprey is an indigenous or invasive species in Lake Ontario (see Emery 1985), it becomes an introduced fish in the upper Great Lakes.

McCann (1984) summarized various steps by U.S. governments to implement effective control of importation and introduction of injurious species. They included the establishment of the National Fisheries Research Center in Gainsville, Florida. A primary concern of that laboratory was "to oversee the development of a research program that will support the use of exotic species for beneficial purposes while protecting the natural environment." That centre maintains a computerized data base on exotic fishes taken in open waters of the continental USA and publishes regular notices entitled Exotic Species Update. In Canada, the Federal–Provincial Transplant Committee passes judgement on, and records, application for the importation and transfer of fishes. Many state, provincial and federal agencies regularly provide updated information for an international registry maintained by the Work Group on Introductions and Transfer of Marine [= aquatic] Organisms of the International Council for the Exploration of the Sea (ICES).

The Great Lakes Fishery Commission (GLFC) is now also involved directly with the problem of introduced aquatic organisms, including fishes. GLFC has an "Introductions Task Area" of the Board of Technical Experts, and a "Ballast Water Working Group." Both these international bodies are addressing problems in the St. Lawrence River and the Great Lakes.

Bailey and Smith (1981) listed 13 species as introduced in the Great Lakes, and an additional six species as recently colonizing the Great Lakes by canal or natural dispersal following introduction. In 1990, E. L. Mills, Cornell University, and J. H. Leach, Ontario Ministry of Natural Resources, prepared for the Exotic Introduction Task Area a report entitled Survey of Non-native Organisms, Their Origin and Impact on the Environment and Native Species of the Great Lakes.

The Introduction of Fishes into Canada

The history of the introduction of fishes into Canada has been extensively documented. It begins with the introduction of common carp into Ontario in 1880. Although many regional works published prior to 1947 (e.g., Dymond 1936; Radforth 1944) listed introduced fishes, the earliest listings for Canada as a whole were Dymond's 1947 checklist of fishes east of the Rocky Mountains and his 1955 summary of introductions (Dymond 1947, 1955). The 1955 summary included four species "not native to Canada that had survived" — *Cyprinus carpio, Carassius auratus, Tinca tinca,* and *Salmo trutta.* Dymond was apparently unaware of the 1924 introduction of *Gambusia affinis* in Banff, Alberta (Mail 1954). Dymond also provided the history for seven species (two unsuccessful at that date) "transferred from one part of North America where they were native, to parts of Canada in which they did not naturally occur." These included — *Oncorhynchus mykiss, O. tshawytscha, O. kisutch, Salmo salar, Salvelinus fontinalis, Osmerus mordax,* and *Micropterus dolomieu.*

Many of the introductions into Canada were in eastern Canada, especially the Great Lakes. As a result, papers dealing with the fish faunas of Ontario or Quebec, and changes to them, are important. Some of these were by Scott (1954, 1957, 1958, 1963), MacKay (1963), Crossman (1968), Legendre et. al (1980), Mongeau et al. (1980), Bergeron and Brousseau (1983), Dumont et al. (1988), and Mandrak (1989, 1990). Most of these cite other publications which provide the records for single species, or single bodies of water.

Other lists of the Canadian fauna indicating introductions were those of Scott and Crossman (1969) and Crossman (1969). Information on fishes introduced into Canada was provided, mainly in the general account of each species, in Freshwater Fishes of Canada and Poissons d'Eau Douce du Canada (Scott and Crossman 1973, 1974). The next summary for Canada was that of Crossman (1984) for the 1981 AFS symposium mentioned above. As such, that list was limited, by the constraints of the symposium, basically to exotic (= foreign) species. However, comments were included on species invading Canada naturally, and on "genetic exotics." Most of the information in that list had been obtained in 1980-81 by summarizing the literature and requesting fisheries agencies in each province and territory to add anything additional known to them. The 1984 summary listed 18 species from foreign countries introduced into Canada (Table 1). These consisted of four salmonids, one umbrid, two cyprinids, one ictalurid, four poeciliids, three cichlids, two anabantids, and one pleuronectid. Of these, nine were indicated as established. Including the European flounder, *Platichthys flesus*, as established was an error. Most of the six individuals reported to date were taken in separate lakes, often

TABLE 1. Exotic species introduced into Canada listed by Crossman (1984). Species with reproductive populations (= established) marked *.

Cyprinidae —	*Carassius auratus** — goldfish *Cyprinus carpio** — common carp
Ictaluridae —	*Noturus insignis** — margined madtom
Umbridae —	*Dallia pectoralis* — Alaska blackfish
Salmonidae —	*Hucho hucho* — Danube salmon *Oncorhynchus masou* — cherry salmon *Oncorhynchus aquabonito** — golden trout *Salmo trutta** — brown trout
Poeciliidae —	*Gambusia affinis** — western mosquito fish *Poecilia latipinna** — sailfin molly *Poecilia reticulata* — guppy *Xiphophorus helleri* — green swordtail
Cichlidae —	*Cichlosoma nigrofasciatum* — convict cichlid *Hemichromis bimaculatus** — jewelfish ?*Pterophyllum scalare* — freshwater angelfish
Anabantidae —	*Betta splendens* — Siamese fightingfish *Trichogaster trichopterus* — threespot gourami
Pleuronectidae —	*Platichthys flessus** — European flounder

The asterisk designating an established population for *Platichthys flessus* in 1984 was an error. Each of six individuals caught at separate times and in different lakes would seem to be an independent introduction.

TABLE 2. Species reported in 1984 as having invaded Canada after being introduced into areas of the United States outside their native range. Province invaded given in brackets.

Clupeidae —	*Alosa sapidissima* (BC)
Cyprinidae —	*Tinca tinca* (BC) *Cyprinus carpio* (in part PQ, ON, SK)
Ictaluridae —	*Ameiurus nebulosus* (BC) *Ameiurus melas* (BC in part)
Esocidae —	*Esox niger* (NB)
Salmonidae —	*Oncorhynchus* spp. — Pacific salmons (NS, NB, PQ)
Centrarchidae —	*Lepomis gibossus* (BC) *Pomoxis nigromaculatus* (BC) *Micropterus salmoides* (BC)
Percidae —	*Perca flavescens* (BC)

in different years, and each would appear to have been an independent introduction. The 1984 summary included a list of species (exotic and otherwise) which had invaded some part of Canada after being introduced outside their native range in the United States. This list (Table 2) included eight eastern species occurring in British Columbia. It did not include the probability that some individual salmonids such as *Oncorhynchus* spp. and *Salmo salar* moved to or "invaded" Canadian waters of the Great Lakes from introductions made in the U.S. McAllister (1990) included a section on introduced fishes in his list of fishes of Canada.

In spite of all the good intentions in defining introduced (Kohler and Courtenay 1986b), and in classifying intentional and unintentional (Courtenay and Taylor 1986) it is still difficult to easily provide maximum information on mechanism of introduction of various species into Canada. None of the classifications adequately includes the natural invasive action so important for the Canadian fauna (see Table 2). the use of ecosystem in regard to transfer also complicates the matter. Lake Ontario and Lake Superior are part of the Great Lakes but could be considered different ecosystems.

TABLE 3. Recent imports of live freshwater fishes in British Columbia and their source. Forage species introduced to support introduced sportfishes are marked *.

Petromyzontidae spp. (WA or CA)	*Esox lucius* (YT, AB)
Acipenser transmontanus (OR, CA)	*Oncorhynchus keta* (AK, YT)
Amia calva (ON)	*O. mykiss* (ON, WA, CA, Norway)
Hiodon alosoides (AB)	*O. tshawytscha* (YT, OR, WA)
Anguilla rostrata (NF, PQ, NY, in transit only)	*Salmo salar* (WA, Scotland)
Couesius plumbeus (AB)*	*Salvelinus alpinus* (MB, AK)
Platygobio gracilis (AB)*	*Thymallus arcticus* (YT, AK, NT)
Notropis hudsonius (AB)*	*Percopsis omiscomaycus**
Pimephales promelas (ON)	*Lota lota* (NT)
Richardsonius balteatus (AB)*	*Culaea inconstans* (AB)*
Catostomus catostomus (AB)*	*Lepomis macrochirus* (MA)
C. commersoni (AB)*	*Perca flavescens* (AB)
Ictalurus punctatus (ID)	*Tilapia* spp. (CO, ID, TX, FL, Philippines)

Some idea of the extent of transfer, the variety of species involved, and the sources from which they were derived is apparent in a list (Table 3) of fishes recently imported into British Columbia. That list does not include species involved in transfer applications which were not approved.

In the final summary of introduced fishes in Canada (Table 4), I have attempted to follow the 1986 definitions but include as much information as possible. To do this, I have divided Intentional into — (1) authorized (IA), and (2) by fish hobbyists (IB). I have divided unintentional introductions into — (1) escapes and other unauthorized releases (U), (2) invasive, without man's assistance (UN), (3) invasive with man's assistance (UM), (4) associated with transport and use of bait (UB), and (5) in some way associated with large vessels including their ballast (UV). This is similar to a scheme provided by Mandrak (1990) for Ontario only. However, there will always be differences in the way various authors interpret indefinite records of rare species and those referred to as transfers. As a result, the notations in Table 4 will not completely agree with those of other authors (e.g., Mandrak 1990).

This 1990–91 summary uses the past literature, the list from Crossman (1984) and various records since 1984. It also includes the results of a resurvey, 1989, of the federal and provincial fisheries agencies in the provinces and territories. Each agency was asked to return information on *any* kind of introduction that had occurred since 1981. This new information is presented here by provinces. When known, the source of the introductions is provided in brackets using the two-letter code for provinces and states. In certain cases, the federal record of transfer of species included instances not known by the agency in the receiving province. All appropriate items were also included in Table 4.

Newfoundland

There have been reports of *Oncorhynchus mykiss* in Conception Bay and Bay d'Espoir as escapes from cage culture. These were apparently triploid females. This species has been imported (from ON, PE) for aquaculture. Pink salmon, *O. gorbuscha*, (from BC), *Salmo salar* (from NS, NB) and *Salvelinus*

TABLE 4. A list to April 1991 of species and hybrids "introduced" into various provinces and territories. Entries include those known, or thought to be, unsuccessful. See end of table for symbols.

Families and Species	Provinces and Territories											
	NF & LB	NS	PE	NB	PQ	ON	MB	SK	AB	BC	NT	YT
Petromyzontidae												
Petromyzon marinus						UM UN						
Lepisosteidae												
Lepisosteus platyrhynchus						IB						
Amiidae												
Amia calva						UB						
Hiodontidae												
Hiodon alosoides										IA?		
Anguillidae												
Anguilla rostrata						UM UV?		IA	UM			
Clupeidae												
Alosa pseudoharengus					UN UM	UN UM						
A. sapidissima					UM?	IA				IA		
Dorosoma cepedianum						UM?						
Cyprinidae												
Campostoma anomalum						UN? UB?						
Carassius auratus		IB		IB?	U UM?	IB? UM?	IBU?	IB	IB	IB		
Couesius plumbeus										IA		
Ctenopharyngodon idella						UM U?			IA			
Cyprinella spiloptera							UN					
Cyprinus carpio				IA	UM?	IA UM?	UN? IA?	UM?		IA UM		
Luxilus chrysocephalus						UB						
Nocomis biguttatus						UB						
N. micropogon						UB						
Notemigonus crysoleucas			IA	UN?		UB						
Notropis atherinoides						U UB?						
N. buchanani						UN?						
N. heterodon							UN					
N. hudsonius								IA		IA		
N. photogenis						UN?						
N. texanus							UN					
N. sp.								IA				
Pimephales promelas						UB?						
Platygobio gracilis										IA		
Richardsonius balteatus									U	IA		
Scardinius erythrophthalmus						UM						
Tinca tinca										UM IA		
Catostomidae												
Catostomus catostomus										IA		
C. commersoni								IA		IA		
Erimyzon sucetta						UN?						
Hypentelium nigricans						UB						
Ictiobus cyprinellus						UN		IA				
I. niger						UN						
Minytrema melanops						UN						
Moxostoma erythrurum							UN?					
Characidae												
Colossoma sp.						IB						
C. cf. *bidens*						IB						
Ictaluridae												
Ictaluridae								IA				
Ameiurus melas							UM			UM		
A. nebulosus							UM			UM IA		
Ictalurus punctatus							UM			IA?		
Noturus flavus							UN UM					
N. gyrinus							UM					
N. insignis					UB	UB						
N. stigmosus						UN UB?						
Pylodictis olivaris						UN						
Loricariidae												
Panque nigrolineatus						IB						

TABLE 4. (*Continued*)

Families and Species	Provinces and Territories											
	NF & LB	NS	PE	NB	PQ	ON	MB	SK	AB	BC	NT	YT
Esocidae												
Esox a. americanus					UM							
E. lucius								IA		IA		
E. masquinongy				UM	IA		IA UN					
E. niger		IA		UM IA?	UM?							
Umbridae												
Dallia pectoralis						IA						
Osmeridae												
Osmerus mordax	IA			IA	UM	UM UB	UM?	IA				
Salmonidae												
Coregonus artedi								IA	IA			
C. clupeaformis	IA				IA		IA	IA	IA	IA		
C. lavaretus					IA?							
Hucho hucho					IA							
Oncorhynchus aguabonita									IA	IA		
O. clarki					U	IA?	IA	IA	IA		IA	
O. gorbuscha	IA	UM		UM	UM	U IA						
O. keta						IA				IA		
O. kisutch		UM		UM	UM	IA		IA	IA			IA
O. masou						IA						
O. mykiss	IA U	IA	IA	IA U	IA UM	IA UM	IA	IA U	IA	IA	IA	IA U
O. mykiss (Palamino)						UM						
O. mykiss (Skamania)						IA UM						
O. mykiss (Tagworker)						IA	IA					
O. nerka					IA	IA	IA	IA	IA	IA		
O. tshawytscha		UM		IA UM	UM	IA UM				IA		
Salmo salar	IA	IA	IA	IA	IA	IA UM	IA?	IA	IA	IA U		
Salmo trutta	IA UN	IA		IA	IA UM	IA	IA	IA	IA	IA		
S. trutta microstigma					IA							
Salvelinus alpinus	IA	IA	IA	IA		IA U	IA	IA	IA	IA	IA	
S. fontinalis		IA	IA	IA		IA	IA	IA	IA	IA	IA	
S. malma									IA	IA		
S. namaycush						IA		IA	IA			
O. clarki lewisi × *O. mykiss*										IA?		
O. mykiss × *H. hucho*					IA							
Salmo salar? × *S. trutta*	IA											
Salmo trutta × *Salvelinus fontinalis*				IA				IA	IA?			
Salvelinus fontinalis × *S. alpinus*									IA			
S. fontinalis × *S. malma* or *S. confluentus*									IA	IA		
S. fontinalis × *S. namaycush*				IA	IA	IA	IA	IA	IA	IA	IA	
(S. f. × *S. n.)* × *S. namaycush*						IA						
S. namaycush × *S. malma* or *S. confluentus*									IA	IA?		
Thymallus arcticus					IA	IA	IA	IA		IA		
Percopsidae												
Percopsis omiscomaycus										IA		
Gadidae												
Lota lota										IA		
Cyprinodontidae												
Fundulus notatus						IB? UN?						
Poeciliidae												
Gambusia affinis						IA	IA		IA	IA?		
Poecilia latipinna									IB			
P. reticulata									IB			
Xiphophorus helleri									IB	IA?		
Gasterosteidae												
Gasterosteidae								IA				
Apeltes quadracus						UV?						
Culaea inconstans										IA		
Gasterosteus aculeatus						UB UV?			U	IA		U
Cottidae												
Cottus rhotheus									U? UB?			

TABLE 4. (*Concluded*)

Families and Species	Provinces and Territories											
	NF & LB	NS	PE	NB	PQ	ON	MB	SK	AB	BC	NT	YT
Percichthyidae												
Morone americana						UM						
M. chrysops						UM	UN? UM?					
Centrarchidae												
Ambloplites rupestris						UM						
Lepomis gibbosus					IA					UM IB IA		
L. gulosus						UN						
L. humilis						UN						
L. macrochirus							IA? U	IA				
Micropterus dolomieu		IA			IA UM	IA	IA	IA	IA	IA	UM IA	
M. salmoides						IA	IA	IA	IA	UM		
Pomoxis annularis							UN UM	IA				
P. nigromaculatus						UM IA	UN IA	IA		UM IA?		
Percidae												
Etheostomatinae								IA				
Perca flavescens								IA	IA	UM IA		
Stizostedion vitreum						IA		IA	IA	UM IA	IA	
Stizostedion sp.					IB?							
Cichlidae												
Astronotus ocellatus						IB						
Cichlasoma nigrofasciatum									IB			
C. managuense						IB						
Hemichromis bimaculatum									IB			
?Pterophyllum scalare									IB?			
Gobiidae												
Neogobius melanostomus						UV						
Anabantidae												
Betta splendens									IB			
Trichogaster trichopterus									IB			
Pleuronectidae												
Platichthys flessus						UV						

Symbols: IA - authorized introduction including transfer from one ecosystem to another in the same province.
IB - released intentionally by fish hobbyist.
U - unintentional release including escape from fish culture facility, and unauthorized releases.
UB - unintentional as a result of release of bait.
UM - unintentional, invasive as a result of man's actions (canals, etc.), including after intentional release elsewhere (e.g., USA).
UN - unintentional, invasive naturally rather than by some man-made interference.
UV - unintentional, via vessel ballast water, etc.

alpinus (from LB, NB, MB) were imported for aquaculture or cage culture.

Nova Scotia

Oncorhynchus mykiss were imported (from WV, WA, ON, PQ, PE) for recreational fishing and aquaculture. *Salmo salar* was imported (from ME, NB) for aquaculture and brood stock. *Salvelinus fontinalis* (from ME) was used to establish a recreational fishery, and *S. alpinus* (from LB) was imported for aquaculture.

Prince Edward Island

The provincial agency reported that no additional species had been purposely released in public waters since 1981. *Salvelinus alpinus* had been imported and was being raised in aquaculture experiments and the likelihood of escape was mentioned.

The Federal/Provincial summaries of transfer of live fishes indicated that in 1987–88 *Oncorhynchus mykiss* had been imported (from WV) for public fisheries, and for aquaculture (from WA, ON, PQ). *Salvelinus fontinalis* had been brought in (from ON, PQ), as had *Salmo salar* (from NB) for aquaculture.

New Brunswick

Rainbow trout, *Oncorhynchus mykiss*, were imported (from ON, PQ, PE, WA) for aquaculture and have spread to public waters. Brook trout, *Salvelinus fontinalis*, have been brought in (from ON, PQ, ME) for aquaculture. Splake, *S. fontinalis* × *S. namaycush*, have been released for a recreational fishery. Arctic char, *S. alpinus*, has been both imported (from MB), and transferred to new locations in the province, for aquaculture and to establish a second viable population. The hybrid *S. alpinus* × *S. fontinalis* has been released in several locations for a recreational fishery. The rainbow smelt, *Osmerus mordax*, has been transferred to new locations in the province as forage for Atlantic salmon, *Salmo salar*.

Quebec

Information on past introductions is available in Dumont et al. (1988) and in other recent references provided in the text. The only information received concerning importations since

1981 involved *Oncorhynchus mykiss* (from PE, ON) for aquaculture, and two whitefishes for research, *Coregonus lavaretus* (from Europe) and *C. clupeaformis* (from ON).

Ontario

A potential major problem recently has been the apparent international transport (both ways) of bait fishes between at least Michigan, New York and Ontario. There are indications that large quantities of the fathead minnow, *Pimephales promelas*, were being imported from New York. A supposed "special strain" of *Notropis atherinoides*, emerald shiner, was also being trucked in from the U.S. and sold in Ontario. A Toronto aquarium wholesaler received a shipment of *Carassius auratus* from Pennsylvania which contained an individual tentatively identified as the rudd, *Scardinius erythropthalmus*. This European species is now reared as bait in New York state, has been captured on the U.S. side of Lake Ontario and the St. Lawrence River, and is superficially almost indistinguishable from the indigenous golden shiner, *Notemigonus crysoleucas*.

The bait industry in Ontario involves transport of fishes within the province. This creates the risk of bait pail transfer from one ecosystem to another. There is the added risk now of bait transferred from the Great lakes carrying adults or veligers of the zebra mussel into waters beyond the Great Lakes. The Ontario Ministry of Natural Resources has, or is, developing new guidelines and regulations to control these problems.

Since the 1981 summary (Crossman 1984) of introductions two species of fishes native to Eastern North America have been established in Ontario waters of Lakes Huron and Superior. The species are threespine stickleback, *Gasterosteus aculeatus* (Stedman and Bowen 1985), and the fourspine stickleback, *Apeltes quadracus* (Holm and Hamilton 1988). Since the threespine stickleback is native to Lake Ontario, it could have been moved by bait bucket or ships' ballast. The fourspine stickleback is restricted to coastal waters and is more likely to have arrived in ballast water.

The European flounder, *Platichthys flessus*, was included in the 1984 summary on the basis of records from Lake Erie in 1974 and 1976. Since then there have been five individual records for Ontario waters of Lakes Erie, Huron, and Superior in 1981–88. Each would appear to be an independent ballast water introduction.

Salmo salar is still being imported (from NB, NS, MA, NY and Scotland) to establish that species in Ontario. The "Skamania" strain of *Oncorhynchus mykiss* was imported (from IN) for introduction into Lake Huron and the "Tagworker" strain (from MB) for aquaculture and a brood stock development. *Salvelinus alpinus* was imported (from MB) for brood stock development.

Manitoba

Cutthroat trout, *Oncorhynchus clarki*, were introduced into Duck Mountain and Whiteshell Provincial Parks but there may have been no survival. Rainbow trout, *O. mykiss*, were imported (from AB) to support a stocking programme. Kokanee, *O. nerka*, were imported (from AB) to support a stocking programme. Kokanee, *O. nerka*, were introduced (from CO) into two lakes to replace an unsuccessful earlier introduction. Arctic char, *Salvelinus alpinus*, were introduced into Duck Mountain Provincial Park (Glad Lake?) but survival is unknown. Eggs of Atlantic salmon, *Salmo salar*, were imported (from NB) for rearing for marketing. The blackchin shiner, *Notropis heterodon*, the weed shiner, *Notropis texanus*, and the golden redhorse, *Moxostoma erythrurum*, would appear to have invaded from the south.

Saskatchewan

Oncorhynchus clarki lewisi yearlings and fingerlings from the Yellowstone and Snake rivers in the U.S. were planted in Shirley Lake, NW of Prince Albert, and in Little Raspberry Lake in Meadow Lake Provincial Park. *Salmo salar* (from ME) had been imported in 1988 and 1989 for brood stock in private hatcheries, and for sport fisheries. This species was released into Brightsand Lake, SW of Meadow Lake. "Tiger trout" (*Salmo trutta* × *Salvelinus fontinalis*) was reported as "new but not introduced" (= of local origin?). This hybrid was released in 1988 into six small lakes in central Saskatchewan. *Micropterus dolomieu* (from ON) was introduced (1983–86) into the Oyama Reservoir near Regina, and *M. salmoides* (from MB) into Boundary Reservoir near Estavan.

Alberta

Arctic char, *Salvelinus alpinus*, had been imported in 1989 by a commercial fish farmer. An anadromous population of Dolly Varden, *Salvelinus m. malma*, from Alaska was introduced into Chester Lake. Polyploid individuals of the Amur carp, *Ctenopharyngodon idella*, were stocked in 1988 in self-contained potholes near Lethbridge to test for vegetation control. The redside dace, *Richardsonius balteatus*, had been unintentionally released in a pothole sportfishery lake in the Oldman River Watershed. There was an unauthorized introduction of the threespine stickleback, *Gasterosteus aculeatus*, into Hasse Lake prior to 1980 (Nelson and Harris 1987). An additional population of smallmouth bass, *Micropterus dolomieu*, with limited evidence of reproduction had been reported from Island Lake.

British Columbia

As a result of the tremendous increase in commercial aquaculture, the importation of fishes into B.C. has been extensive. Fortunately, the control exerted by the Federal/Provincial Transplant Committee makes records of them available.

Those records indicated that 19 plus species (some were grouped as *Tilapia* sp., or lampreys) of fishes have been imported alive from 18 locations (Table 3). These have been included to indicate the variety of fishes being imported into one province. The sources include Canadian provinces and territories, U.S. states, the Caribbean, Norway, Scotland, and the Philippines. The fishes were imported for cage culture, research, bioassay, education, private and public aquaria, enhancement of populations, and brood stock.

Many of these imports are not intended for release, but some species with a potential for survival were included in Table 4.

In addition to the above, there were several other records of interest. Kokanee, *Oncorhynchus nerka*, were reported from the Simpson and Kootenay rivers near and in Kootenay National Park. These result from the introduction of that species in the Bull River, B.C. which populated Lake Koocanusa (Libby Dam), Kootenay River, Montana. The black crappie, *Pomoxis nigromaculatus*, now occurs in the lower Fraser River, and lower Okanagan River. The walleye, *Stizostedion vitreum*, recently moved into the Columbia River near Trail, following their introduction in Roosevelt Reservoir in Washington. The

yellow perch, *Perca flavescens*, now occurs in Swan Lake near Dawson Creek, and was introduced (from AB) in 1981 and 1986 into Charlie Lake, near Fort St. John (Baker and Hammond 1987). Smaller numbers of *Esox lucius*, and *Lota lota* and large numbers of individuals of eight species of forage fishes (* in Table 3) to support the sportfishes were part of the 1986 introduction from Alberta. Of these, only the spotfin shiner, *Notropis hudsonius*, did not occur previously in nearby waters.

Northwest Territories

It has been reported that the demand for quality roadside access fishing opportunities had exceeded the supply, requiring establishment of a more active programme of introductions and transfer.

Brook trout, *Salvelinus fontinalis*, was the first fish to be introduced (from AB) in these territories in Seven Mile Lake in 1949 and in 1960 or 1961 in the Little Buffalo River. Splake were introduced into Seven Mile Lake in 1964 (Nelson and Paetz 1972). Brook trout (or splake?) was introduced in 1971 into Polar Lake near Hay River. In 1977 the same lake received the first of several stocks of *Oncorhynchus mykiss*. That species had been introduced into Seven Mile Lake in 1959. The same species was unsuccessfully stocked in Lake 9 near Polar Lake, and introductions were made in 1982, 1985, 1990 in Upper Cabin Lake on the Ingraham Trail east of Yellowknife, and a barrow pit south of Hay River. The cutthroat trout, *Oncorhynchus clarki*, was introduced in Seven Mile Lake in 1964. *Salvelinus alpinus*, from the Tree River, was moved in 1989 into several waters in the Hay River and Yellowknife areas. *Stizostedion vitreum* (from NT) was transferred in 1985(?) into Sandy Lake SE of Hay River (unsuccessful?).

Other than BC, these territories were the only area reporting the establishment (in 1987) of a Cooperative Workplan (DFO/GNWT) to carefully assess waters for potential stocking, and to establish a disease free brood stock of *Salvelinus alpinus*.

Yukon Territory

Gasterosteus aculeatus was discovered to be established in Long and Gloria lakes and assumed to have been brought in with the *Oncorhynchus kisutch* and *O. mykiss* introduced there starting in 1977 (from BC) by means of annual or biennial stocking. *O. mykiss* was also introduced illegally in Watt's Lake at the headwaters of the Liard River.

Yukon Territory, like NWT, is establishing a committee to oversee proposed introductions.

Discussion

At present, it appears that the list of species that have been brought to Canada from other countries, have invaded Canadian waters, or have been moved from one "ecosystem" to another within Canada includes 92 species and 13 additional "forms" (unusual subspecies, prominent selected varieties, and hybrids). These fishes fall into 27 families (Table 4). Anyone who has attempted a listing such as this will recognize that in spite of careful checking of the literature, text, and tables, there will be errors and unintentional omissions. I hope those who find obvious shortcomings will notify me so the records can be corrected. In addition, some interpretations of transfers within Canada (as IA) will seem unusual without the clarifying information.

The initiatives of the Introduced Fish Committee of the American Fisheries Society, recommendations made to U.S. state and federal governments, and the actions of the Canadian federal-provincial control groups have gone a long way to develop checks and protocols to govern requests for introductions as now more broadly defined (see Porter and Goldthwaite 1987). Considerably more must be done, since notes here on species (and forms) recently "imported" into some part of Canada indicate that the amount of this activity is still extensive. The reports returned (e.g., Yukon Territory) make it obvious that more control, and probably more centralized control and recording, is necessary for a clear picture of what is occurring. This is particularly true since confusion will arise until everyone is familiar with, and using, the newer definitions of the term introduced.

There are a number of pressures that increase the potential for unwanted impacts from introduced fishes. Some of these in Canada are — (1) increase in numbers of fish hobbyists, a trend toward "native" species, and the habit of selling or exchanging specimens or releasing them in public waters; (2) ongoing interest by anglers for new species, hatchery support of existing populations, and in angling opportunities where none existed previously; (3) the import of bait fishes and ongoing transfer of them from one area to another; (4) the escape of species transferred or imported for cage culture or other types of aquaculture; (5) the selective breeding or genetic adjustment of species to emphasize traits desired by man, and the results of the cross mating (or attempts to mate) with the "wild" form of that species or related species; (6) climatic warming increasing the existing tendency for southern species to move north into Canadian waters; and (7) the more recently important inoculations of Canadian waters with "foreign" species assumed to have been transferred in ships' water ballast. Within biologically sound limits, the societal demands among these should be met. However, people in all walks of life must be made more aware of the extent to which distributions have been carried out, of the need for study and careful documentation of any authorized in future, and of the potential for irreversible environmental impact of even a single unwise "exotic" (e.g., zebra mussel).

It was once popular to seek guidance in Confucian philosophy. In a statement of caution concerning potential impacts of transgenic fishes, Kapuscinski and Hallerman (1990) cited the Taoist philosophy of Lao Zu (or the Book of Lao Zu) in the expression "Better a foot behind than an inch too far ahead." Another expression from the same source that also applies to introductions is "One should know the laws of nature and conduct ones activities in accordance with them." This harks back to Regier's (1968) very early warnings.

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Genetic Implications of Introducing Florida Largemouth Bass, *Micropterus salmoides floridanus*[1]

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Stocks of northern largemouth bass (NLMB), *Micropterus salmoides salmoides*, Florida largemouth bass (FLMB), *M. s. floridanus*, and both reciprocal F_1 hybrids were produced through natural spawning; the genetic composition of each stock was confirmed electrophoretically, and experimental populations established. One set of experimental populations (P1 and P2) contained as broodstock equal numbers of adult NLMB and FLMB, whereas the other set (H1 and H2) initially contained equal numbers of adults of both reciprocal F_1 hybrids and both pure subspecies. Each year-class produced experimentally were sampled and individuals analyzed genetically to determine their parentage. Initially, much of the YOY production in P1 and P2 was composed of small FLMB that did not survive winter well; once naturally produced F_1 hybrids entered the breeding pool, most offspring were F_x hybrids, and the population became heavily introgressed. In H1 and H2 introgression began with the production of the first year-class. Within each year-class NLMB produced in all ponds were significantly larger than all other genotypes, but it appears likely that after only a few generations, production of pure NLMB ceases, all individuals being F_x hybrids. Results illustrate the potential negative impacts of introducing FLMB or hybrids between it and NLMB into waters within or contiguous to the native range of the northern subspecies.

On a produit des stocks d'achigans à grande bouche du Nord (AGBN), *Micropterus salmoides salmoides*, d'achigans à grande bouche de la Floride (AGBF), *M. s. floridanus*, et des deux hybrides réciproques F_1 par frai naturel; on a vérifié la composition génétique de chacun des stocks par électrophorèse et on a défini les populations expérimentales. Un groupe de populations expérimentales (P1 et P2) avait pour stock reproducteur un nombre égal d'adultes AGBN et AGBF, alors qu'un autre groupe (H1 et H2) comprenait initialement un nombre égal d'adultes des deux hybrides réciproques F_1 et des deux sous-espèces pures. On a échantillonné chaque classe d'âge produite au cours de l'expérience et on a analysé génétiquement chaque poisson pour déterminer son ascendance. Initialement, une grande partie de la production de jeunes de l'année dans les populations P1 et P2 se composait d'AGBF de petite taille qui ont survécu difficilement à l'hiver; après l' introduction d'hybrides F_1 produits naturellement dans le groupe de reproducteurs, la plupart des descendants ont été des hybrides F_x, et la population est devenue fortement introgressive. Dans les populations H1 et H2, l'introgression a commencé à se manifester dans la classe des poissons âgés d'un an. Dans chacune des classes d'âge, les AGBN de tous les étangs étaient sensiblement plus grands que tous les autres génotypes, mais il semble vraisemblable que la production d'AGBN pur cesse après seulement quelques générations et que tous les individus soient alors des hybrides F_x. Les résultats illustrent les effets néfastes possibles de l'introduction d'AGBF, ou d'hybrides d'AGBF et d'AGBN, dans des eaux qui appartiennent ou qui sont contiguës à l'aire de distribution de la sous-espèce nordique.

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The original native range of the largemouth bass, *Micropterus salmoides*, consisted of much of the eastern United States, as well as portions of southeastern Canada and northeastern Mexico. Over the last century, however, this range has been expanded considerably through extensive stocking programs (MacCrimmon and Robbins 1975) that have often progressed with little consideration given to their genetic and/or ecological consequences. Management programs that are of particular concern are those that involve the introduction of the Florida subspecies, *M. s. floridanus*, into native populations of the northern subspecies, *M. s. salmoides*. Great claims have been made by outdoor writers and agency personnel, alike, as to the benefits of introducing Florida largemouth bass (FLMB) into waters outside of peninsular Florida. To date, however, positive effects of such programs have only been assumed, not documented. Consequently, the long-term effects of such stocking practices on the native populations of largemouth bass in such waters have not been evaluated.

Since Bailey and Hubbs (1949) originally described the two subspecies of largemouth bass, a number of studies have compared their survival and growth under controlled field conditions (Clugston 1964; Addison and Spencer 1972; Inman et al. 1976; Zolczynski and Davies 1976; Smith and Wilson 1981; Wright and Wigtil 1981; Isely et al. 1987; Williamson and Carmichael 1990; Philipp and Whitt 1991. The findings of these studies, however, often disagree. This lack of consensus may result from the lack of data describing the genetic identity of the largemouth bass stocks used in all but the three most recent of these reports. Philipp et al. (1981, 1983) developed an elec-

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trophoretic method for determining the percentage contribution of each of the two subspecific genomes within any given population. This procedure has been confirmed and even expanded (Carmichael et al. 1986; Hallerman et al. 1986; Williamson et al. 1986). Without verification of the subspecific (or hybrid) status of these stocks, few conclusions, if any, are warranted. A number of other studies have attempted to assess the effects of introducing the Florida subspecies into existing populations of the northern subspecies in California (von Geldern and Mitchell 1975; Bottroff and Lembeck 1978; Moyle and Holzhauser 1978; Pelzman 1980) and in Texas (Inman et al. 1976; Kulzer et al. 1985; Maceina et al. 1988; Maceina and Murphy 1988). Unfortunately, the genetic purity of the "Florida" largemouth bass introduced into these states is questionable. This unknown genetic status of the donor largemouth bass populations, together with the lack of initial genetic characterization of the recipient populations, preclude assessment of the genetic effects of these introductions.

I propose that fish introduction programs involving stock transfers, particularly those in which Florida largemouth bass are being propagated and stocked into waters outside of peninsular Florida, have deleterious fitness consequences for the recipient populations. The purpose of this study was to produce genetically confirmed stocks of each subspecies of largemouth bass, as well as both reciprocal F_1 hybrids, and to evaluate their relative reproductive success in experimental populations established in central Illinois.

Methods

Genetic Analysis

Protein electrophoretic analysis was conducted as described in Philipp et al. (1979) using vertical starch gels and histochemical staining for isocitrate dehydrogenase, aspartate aminotransferase, and malate dehydrogenase. Nomenclature used was that proposed by Shaklee et al. (1990).

Stock Production

Adult northern largemouth bass (NLMB) were collected from Bone Lake, Wisconsin. All individuals analyzed from this population contained only the *IDHP*-1*^{100} (formerly Idh-B^1), and *sAAT*-2*^{100} or *sAAT*-2*^{110} (formerly Aat-B^1 or B^2) alleles, characteristic of the northern subspecies (Philipp et al. 1983). Adult Florida largemouth bass (FLMB) were collected from Lake Dora, Florida. All individuals analyzed from this population contained only the *IDHP*-1*^{114} (formerly Idh-B^3) and *sAAT*-2*^{126} or *sAAT*-2*^{139} (formerly Aat-B^3 or B^4) alleles, characteristic of the Florida subspecies (Philipp et al. 1983). Thus, electrophoretic analysis confirmed the subspecific purity of the broodstock used in these experiments. In addition, through selection of broodstock parents, the NLMB were fixed for the *sMDH*-B*^{100} (formerly Mdh-B^1) allele, whereas the FLMB were fixed for the *sMDH*-B*^{140} (formerly Mdh-B^2) allele.

These broodstocks were used to produce four genetically defined stocks of largemouth bass, i.e., NLMB, FLMB, and both reciprocal F_1 hybrids, NLMB ♀ × FLMB ♂ (N × F) and FLMB ♀ × NLMB ♂ (F × N); adults of appropriate sex and subspecies were stocked into four 0.08-ha ponds, and spawning occurred in all ponds. Ponds were drained, young (40–60 mm TL) were recovered from each pond, and electrophoretic analysis of 100 fingerlings from each stock confirmed their genetic composition. A fin on each fish was clipped for visual identification of stock identity (NLMB = right pectoral; N × F = right pelvic; F × N = left pelvic; FLMB = left pectoral) and grown to maturity together in a series of research ponds at the INHS Aquatic Research Field Laboratory in Champaign, IL.

TABLE 1. Stocking protocols for experimental populations. Total lengths (mm) and weights (g) are mean ± SD.

Pond	Stock	*N*	Total length[a]	Weight[a]	Date
P-1 (1.2 ha)	NLMB	46	285 ± 16	295 ± 52	03-15-82
	FLMB	46	277 ± 22	271 ± 60	03-15-82
P-2 (0.5 ha)	NLMB	10	384 ± 40	856 ± 261	03-30-84
	FLMB	10	371 ± 39	721 ± 234	03-30-84
H-1 (2.0 ha)	NLMB	40	272 ± 15	270 ± 47	04-02-83
	N × F	40	275 ± 12	285 ± 61	04-02-83
	F × N	40	265 ± 19	262 ± 67	04-02-83
	FLMB	40	270 ± 14	261 ± 45	04-02-83
H-2 (1.1 ha)	NLMB	12	302 ± 27	406 ± 105	03-29-84
	N × F	12	297 ± 20	382 ± 110	03-29-84
	F × N	12	294 ± 28	386 ± 75	03-29-84
	FLMB	12	291 ± 35	375 ± 120	03-29-84

[a]ANOVA indicated there were no differences in total length or weights of any of the stocks introduced into a single pond.

Establishment of Experimental Populations

Two sets of experimental populations (two replicates each) were established in research ponds located in central Illinois that contained no other fish; numbers, lengths, weights, and stocking dates are given in Table 1. The first set (P-1 and P-2) was established using equal numbers (both sexes) of only the two pure subspecies, NLMB and FLMB. The second set (H-1 and H-2) was established using equal numbers (both sexes) of not only both pure subspecies, NLMB and FLMB, but also of both reciprocal intersubspecific F_1 hybrids, N × F and F × N.

Initial introductions were made in early spring, after any change of winter-associated mortality had passed, but well prior to the onset of normal spawning activity among largemouth bass. A natural prey base of bluegill (*Lepomis macrochirus*), fathead minnows (*Pimephales promelas*), and lake chubsuckers (*Erimyzon sucetta*), was also stocked into each pond. All four largemouth bass populations were allowed to reproduce naturally, with all four being successful in the first and all succeeding years of the study. The populations in each pond were also allowed to experience natural mortality throughout the entire study; angling harvest in these ponds was prohibited.

Sampling Offspring Production

Following establishment of each population, largemouth bass were sampled using a combination of seining and electrofishing techniques. That is, each year-class was sampled first as YOY and if numbers permitted, again in successive years. Age determination of older individuals was accomplished through analysis of scale and/or otolith annual rings. Individuals were weighed, measured, and frozen at −20°C until electrophoretic analyses were performed, as described in Philipp et al. (1979). Stock parentage (NLMB, FLMB, F_1 hybrid, or F_x hybrid) for each offspring was assigned based upon its genotype at the three diagnostic loci, *IDHP*-1*, *sAAT*-2*, and *sMDH*-B*. It is recognized that some F_x hybrids, backcrossed individuals or individuals from some F_2, F_3, . . . F_n generation will have combined genotypes at these three loci that are identical to NLMB,

TABLE 2. Genetic composition and size of the YOY LMB produced in population P-1. Total lengths (mm) and weights (g) are mean ± SD. Letters designate significant differences between stocks at $P < 0.05$ (Scheffe's F-test). All comparisons are limited to stocks within a single collection.

		Collection 1				Collection 2			
Year-class	Stock	*N*	%	Total length	Weight	*N*	%	Total length	Weight
				08-11-82				*10-02-82*	
1982	NLMB	20	20	108 ± 16A	18.0 ± 6.7A	31	31	125 ± 23A	28.4 ± 9.6A
	F_1	16	16	80 ± 13B	7.4 ± 4.2B	19	19	104 ± 11B	14.1 ± 4.4B
	FLMB	64	64	82 ± 15B	7.2 ± 4.0B	50	50	102 ± 17B	12.9 ± 7.2B
				08-14-83				*11-04-83*	
1983	NLMB	6	6	79 ± 12A	6.0 ± 3.0A	11	31	179 ± 10A	91.2 ± 19A
	F_1	7	7	61 ± 11B	2.7 ± 1.5B	7	20	147 ± 20B	38.1 ± 16B
	FLMB	87	87	52 ± 9B	1.5 ± 0.8C	17	49	142 ± 31B	34.5 ± 17B
				08-06-84				*10-21-84*	
1984	NLMB	76	76	53 ± 5.5A	1.9 ± 0.68A	17	35	115 ± 13A	18.3 ± 6.2A
	F_1	5	5	47 ± 4.4B	1.1 ± 0.08B	6	13	91 ± 13B	9.2 ± 4.2B
	F_x	7	7	43 ± 6.2B	1.1 ± 0.49B	8	17	86 ± 13B	8.4 ± 3.7B
	FLMB	12	12	45 ± 5.6B	1.1 ± 0.45B	17	35	75 ± 12B	4.8 ± 2.4B
				07-31-85				*11-11-85*	
1985	NLMB	26	26	61 ± 8.0A	2.8 ± 0.94A	7	16	100 ± 14A	13.6 ± 1.1A
	F_1	18	18	52 ± 6.3B	1.8 ± 0.57B	11	24	75 ± 10B	5.1 ± 2.0B
	F_x	53	53	48 ± 5.0B	1.5 ± 0.52B	24	53	70 ± 8B	4.2 ± 1.4B
	FLMB	3	3	46 ± 4.5B	1.4 ± 0.48B	3	7	72 ± 3B	4.0 ± 2.4B

TABLE 3. Genetic composition and size of the YOY LMB produced in population P-2. Total lengths (mm) and weights (g) are mean ± SD. Letters designate significant differences between stocks at $P < 0.05$ (Scheffe's F-test). All comparisons are limited to stocks within a single collection.

Year-class	Date	Stock	*N*	%	Total length	Weight
1984	09-26-84	NLMB	18	18	78 ± 10A	6.5 ± 1.2A
		F_1	4	4	61 ± 11B	2.7 ± 1.1B
		FLMB	78	78	50 ± 7C	1.7 ± 0.8B
1985	09-12-85	NLMB	4	14	95 ± 6.1A	11.8 ± 2.1A
		F_1	22	76	72 ± 7.5B	4.8 ± 1.3B
		FLMB	3	10	53 ± 2.0C	1.8 ± 0.2C
1986	07-15-86	NLMB	32	64	55 ± 7.1A	2.0 ± 0.67A
		F_1	16	32	34 ± 6.2B	0.8 ± 0.27B
		FLMB	2	4	35 ± 2.1B	0.6 ± 0.05B
1987	07-23-87	NLMB	10	8	80 ± 10A	6.9 ± 2.9A
		F_1	21	18	62 ± 12B	3.4 ± 2.2B
		F_x	82	68	65 ± 9B	3.7 ± 1.4B
		FLMB	7	6	56 ± 10B	2.5 ± 1.3B
1988	07-02-88	NLMB	6	6	38 ± 2.5A	0.45 ± 0.10A
		F_1	6	6	32 ± 2.8B	0.27 ± 0.12B
		F_x	89	85	33 ± 3.1B	0.29 ± 0.09B
		FLMB	4	3	32 ± 0.8B	0.24 ± 0.03B

FLMB, or F_1 hybrids. These F_x individuals would have been misclassified as one of these other stocks. The incidence of this misclassification was most likely minimal over the early few years comprising this study, but where it was possible, it has been highlighted.

Calculation of Genetic Contribution

Genetic contribution by each of the two subspecific genomes to the overall gene pool of the final resulting population was determined from the last year-class produced in each pond during this study. Percentage contribution was calculated as the average frequency of NLMB (or FLMB) alleles at the three diagnostic loci among the YOY sampled from that last year-class.

Results

P-1 and P-2 Populations (NLMB and FLMB Broodstock Only)

Initially, during the first year or two, many of the offspring produced in both P-1 and P-2 were pure FLMB, however, the production of pure NLMB and F_1 hybrids was not negligible (Tables 2–3). The relative abundance of FLMB, but not of F_1

TABLE 4. Genetic composition and size of the 1982 year-class of LMB produced in population P-1 over the 4-yr period, 1982–85. Total lengths (mm) and weights (g) are mean ± SD. Letters designate significant differences between stocks at $P < 0.05$ (Scheffe's F-test). All comparisons are limited to stocks within a single collection.

Date	Stock	N	%	Total length	Weight
10-02-82	NLMB	31	31	125 ± 23A	28.4 ± 9.6A
	F_1	19	19	104 ± 11B	14.1 ± 4.4B
	FLMB	50	50	102 ± 17B	12.9 ± 7.2B
10-07-83	NLMB	25	25	231 ± 45A	208 ± 136A
	F_1	37	37	188 ± 17B	87 ± 27B
	FLMB	38	38	188 ± 15B	79 ± 24B
10-21-84	NLMB	25	32	281 ± 16A	296 ± 64A
	F_1	44	56	255 ± 19B	216 ± 56B
	FLMB	9	12	234 ± 22C	166 ± 48C
06-27-85	NLMB	17	34	333 ± 34A	436 ± 63A
	F_1	27	54	272 ± 16B	310 ± 36B
	FLMB	6	12	240 ± 20C	221 ± 32C

TABLE 5. Genetic composition and size of the 1984 year-class of LMB produced in population P-2 over the 4-yr period, 1984–87. Total lengths (mm) and weights (g) are mean ± SD. Letters designate significant differences between stocks at $P < 0.05$ (Scheffe's F-test). All comparisons are limited to stocks within a single collection.

Date	Stock	N	%	Total length	Weight
09-26-84	NLMB	18	18	78 ± 10A	6.5 ± 1.2A
	F_1	4	4	61 ± 11B	2.7 ± 1.1B
	FLMB	78	78	50 ± 7C	1.7 ± 0.8B
05-24-85	NLMB	52	74	94 ± 9A	11.4 ± 13.8A
	F_1	15	21	87 ± 7B	8.7 ± 2.2B
	FLMB	3	5	66 ± 7C	4.0 ± 1.5B
09-12-85	NLMB	75	85	128 ± 10A	27 ± 7.6A
	F_1	13	15	119 ± 8B	20 ± 4.5B
	FLMB	0	0	NA	NA
07-15-86	NLMB	17	81	214 ± 8A	140 ± 21A
	F_1	4	19	196 ± 8B	91 ± 11B
	FLMB	0	0	NA	NA
07-23-87	NLMB	19	79	300 ± 10A	401 ± 19A
	F_1	5	21	276 ± 11B	272 ± 28B
	FLMB	0	0	NA	NA

hybrids, in the initial year-class decreased precipitously through time, from 50% to 12% in P-1 and from 78% to 0% in P-2, in just 2–3 yr (Tables 4–5). This same pattern of decline for FLMB was observed for all year-classes in all ponds. In both ponds, though, the greatest production during the third year was pure NLMB. This rise in NLMB production most likely results from two things, a greater cumulative overwinter mortality of stocked FLMB and an earlier entrance into the breeding pool of the faster growing NLMB produced in the initial year-class.

When some individuals of the initial year-class of LMB produced in each pond first matured (1984, age 2+ for P-1, and 1987, age 3+ for P-2), F_x individuals began to be produced (Tables 2–3). By the next year, when all individuals of that initial year-class entered the breeding pool, the majority of offspring produced in each pond (53% in P-1 and 85% in P-2) were F_x individuals. The percentage of F_x individuals produced in each successive year-class increased, indicating that total introgression was being approached rapidly.

In addition, for every year-class produced in both P-1 and P-2, the NLMB were significantly longer and heavier at sampling (ANOVA, followed by Scheffe's F-test with $P<0.05$) than all other genotypes (Tables 2–3). For most year-classes, there were no significant differences in size among FLMB, F_1, or F_x hybrid YOY individuals. However, as a given year-class aged, F_1 hybrids became significantly longer than FLMB (Tables 4–5). The growth advantage of the NLMB over other genotypes continued throughout the study.

H-1 and H-2 Populations (NLMB, FLMB, and F_1 Hybrids)

For the first year in H-1, but not in H-2, FLMB made up a major portion of the YOY production (Tables 6–7). In all other years, the majority of YOY production consisted of F_x individuals, as expected, since these ponds were initially stocked with 50% F_1 hybrids. In this initial year-class, the relative abundance of FLMB decreased precipitously, going to 0% in both ponds after the first winter (Tables 8–9). Interestingly, in H-1 but not noticeably in H-2, there was also a dramatic decline in abundance of F_1 and F_x hybrids relative to NLMB. This is most

TABLE 6. Genetic composition and size of the YOY LMB produced in population H-1. Total lengths (mm) and weights (g) are mean ± SD. Letters designate significant differences between stocks at $P<0.05$ (Scheffe's F-test). All comparisons are limited to stocks within a single collection.

Year-class	Stock	N	%	Total length	Weight	N	%	Total length	Weight
				08-10-83				*10-12-83*	
1983	NLMB	9	9	120 ± 9A	24.9 ± 5.9A	21	21	184 ± 8A	84.6 ± 15A
	F_1	35	35	56 ± 13B	2.7 ± 3.6B	17	17	124 ± 42B	30.9 ± 27B
	F_x	24	24	52 ± 16B	2.3 ± 2.7B	26	26	89 ± 23C	9.9 ± 13C
	FLMB	32	32	41 ± 6C	0.9 ± 0.4B	36	36	70 ± 16D	4.3 ± 2C
				08-23-84					
1984	NLMB	4	8	94 ± 5.6A	10.1 ± 1.9A				
	F_1	6	12	67 ± 3.2B	3.7 ± 0.7B				
	F_x	38	76	73 ± 7.3B	4.8 ± 1.4B				
	FLMB	2	4	73 ± 5.7B	5.1 ± 0.5B				
				07-21-85				*11-17-85*	
1985	NLMB	30	30	51 ± 6.5A	1.8 ± 0.69A	37	37	72 ± 18A	5.2 ± 4.2A
	F_1	13	13	45 ± 3.8B	1.3 ± 0.31B	20	20	62 ± 7B	3.3 ± 1.0B
	F_x	55	55	45 ± 4.3B	1.3 ± 0.36B	43	43	61 ± 8B	3.2 ± 1.1B
	FLMB	2	2	43 ± 0.7B	1.0 ± 0.03B	0	0	NA	NA
				08-05-86					
1986	NLMB	5	9	88 ± 5.6A	7.9 ± 1.2A				
	F_1	5	9	51 ± 6.8B	1.0 ± 0.1B				
	F_x	38	74	49 ± 3.0B	1.7 ± 0.1B				
	FLMB	4	8	43 ± 1.7C	1.5 ± 0.2B				

TABLE 7. Genetic composition and size of the YOY LMB produced in population H-2. Total lengths (mm) and weights (g) are mean ± SD. Letters designate significant differences between stocks at $P < 0.05$ (Scheffe's F-test). All comparisons are limited to stocks within a single collection.

Year-class	Date	Stock	N	%	Total length	Weight
1984	09-26-84	NLMB	16	16	70 ± 9A	4.5 ± 2.3A
		F_1	14	14	62 ± 6B	2.9 ± 0.06B
		F_x	67	67	62 ± 5B	2.7 ± 0.6B
		FLMB	3	3	50 ± 2B	2.5 ± 0.5B
1985	09-24-85	NLMB	14	18	95 ± 6.1A	11.8 ± 2.1A
		F_1	9	11	71 ± 17B	5.2 ± 3.2B
		F_x	51	64	71 ± 14B	5.0 ± 2.9B
		FLMB	6	7	68 ± 13B	4.1 ± 2.3B
1986	08-12-86	NLMB	7	7	80 ± 6A	7.1 ± 1.5A
		F_1	21	21	57 ± 5B	2.4 ± 0.1B
		F_x	82	82	58 ± 5B	2.6 ± 0.8B
		FLMB	0	0	NA	NA
1987	07-28-87	NLMB	5	5	88 ± 6A	8.0 ± 1.4A
		F_1	9	9	51 ± 2B	2.1 ± 1.1B
		F_x	83	83	48 ± 3B	1.5 ± 0.2C
		FLMB	3	3	41 ± 1C	0.9 ± 0.1C
1988	07-02-88	NLMB	8	9	41 ± 1.1A	0.79 ± 0.06A
		F_1	8	9	35 ± 1.0B	0.51 ± 0.08B
		F_x	71	79	36 ± 2.6B	0.57 ± 0.13B
		FLMB	3	3	36 ± 1.2B	0.51 ± 0.09B

likely due to the much greater size disparity among the LMB genotypes in H-1 compared to H-2.

As in populations P-1 and P-2, in all of the year-classes produced in H-1 and H-2 the NLMB were significantly longer and heavier at sampling (ANOVA, followed by Scheffe's F-test with $P<0.05$) than all other genotypes (Tables 6–7). For most year-classes (the initial year-class in H-1 being the most notable exception), there were no significant differences in size among the FLMB, F_1, or F_x hybrid YOY individuals. Again, the growth advantage of the NLMB over other genotypes continued as they aged throughout the study (Tables 8–9).

Discussion

Specific allelic combinations and genic arrangements (coadapted gene complexes) that prove advantageous for individual largemouth bass in a given environment will be maintained through natural selection. Through the development of these

TABLE 8. Genetic composition and size of the 1983 year-class of LMB produced in population H-1 over the 3-yr period, 1983–85. Total lengths (mm) and weights (g) are mean ± SD. Letters designate significant differences between stocks at $P < 0.05$ (Scheffe's F-test). All comparisons are limited to stocks within a single collection.

Date	Stock	N	%	Total length	Weight
08-10-83	NLMB	9	9	120 ± 9A	24.9 ± 5.9A
	F_1	35	35	50 ± 13B	2.7 ± 3.6B
	F_x	24	24	52 ± 16B	2.3 ± 2.7B
	FLMB	32	32	41 ± 6C	0.9 ± 0.4B
10-12-83	NLMB	21	21	184 ± 8A	84.6 ± 15A
	F_1	17	17	124 ± 42B	30.9 ± 27B
	F_x	26	26	89 ± 23C	9.9 ± 13C
	FLMB	36	36	70 ± 116D	4.2 ± 2C
08-23-84	NLMB	38	75	242 ± 13A	190 ± 33A
	F_1	8	16	210 ± 32B	139 ± 52B
	F_x	5	9	205 ± 13B	127 ± 22B
	FLMB	0	0	NA	NA
07-21-85	NLMB	23	72	300 ± 12A	396 ± 39A
	F_1	4	13	255 ± 12B	196 ± 34B
	F_x	5	15	243 ± 24B	168 ± 49B
	FLMB	0	0	NA	NA

TABLE 9. Genetic composition and size of the 1982 year-class of LMB produced in population H-2 over the 3-yr period, 1984–86. Total lengths (mm) and weights (g) are mean ± SD. Letters designate significant differences between stocks at $P < 0.05$ (Scheffe's F-test). All comparisons are limited to stocks within a single collection.

Date	Stock	N	%	Total length	Weight
08-04-84	NLMB	21	21	57 ± 10A	2.4 ± 1.3A
	F_1	16	16	47 ± 3B	1.4 ± 0.3B
	F_x	63	63	48 ± 3B	1.5 ± 0.3B
	FLMB	4	4	46 ± 2B	1.2 ± 0.2B
09-26-84	NLMB	16	16	70 ± 9A	4.5 ± 2.3A
	F_1	14	14	62 ± 6B	2.9 ± 0.6B
	F_x	67	67	62 ± 5B	2.7 ± 0.6B
	FLMB	3	3	56 ± 12B	2.5 ± 0.5B
05-24-85	NLMB	28	38	96 ± 18A	14.0 ± 9.9A
	F_1	7	9	78 ± 8B	6.7 ± 2.7B
	F_x	39	53	78 ± 5B	6.6 ± 1.6B
	FLMB	0	0	NA	NA
05-12-86	NLMB	17	26	268 ± 25A	310 ± 54A
	F_1	6	9	203 ± 34B	127 ± 68B
	F_x	43	65	199 ± 26B	118 ± 56B
	FLMB	0	0	NA	NA

coadapted gene complexes, stocks or populations become adapted to their local environments, maximizing their relative fitness. Thus, different populations of largemouth bass inhabiting different environments will evolve different coadapted gene complexes in response to the different selective pressures present, ie. undergo local adaptation. I propose that the introduction of largemouth bass from one environment into a population of largemouth bass in another environment followed by their subsequent interbreeding, will create a new intergrade population with decreased relative fitness compared to the original native population as a result of the disruption of the coadapted gene complexes that had evolved in both stocks. Because northern and Florida largemouth bass evolved in quite different habitats and under quite different selective pressures, we have proposed (Philipp et al. 1981, 1983, 1985; Fields et al. 1987; Philipp and Whitt 1991) that their relative fitness differs greatly among different habitats. This study directly compared the fitness of the two subspecies in the absence and presence of both reciprocal F_1 hybrids in experimental populations established in central Illinois.

Philipp and Whitt (1991) have shown previously that in central Illinois, FLMB, as well as both reciprocal F_1 hybrids, have decreased survival compared to pure NLMB. Here I show that the two subspecies readily interbreed, creating an introgressed population comprised predominantly, if not totally, of F_x hybrid individuals after only a very few generations. The growth and survival characteristics of these F_x individuals are inferior to the pure NLMB. It has been suggested that in a mixed population in Aquilla Lake, Texas, FLMB females showed a growth-related fecundity advantage over NLMB females after 3 yr (Maceina et al. 1988). Unfortunately, this conclusion was based on very small sample sizes of FLMB ($N = 7$) and NLMB

TABLE 10. Genetic contribution of the NLMB and FLMB genomes to the last year-class produced in each pond during the study. Each population was initiated with equal numbers of both subspecies' alleles at the three fixed loci, *IDHP**-1, *sAAT**-2, *sMDH**-B. Contributions are means of all three single locus calculations.

	P-1 (1985)	P-2 (1988)	H-1 (1986)	H-2 (1988)
NLMB	60.8	59.5	63.3	53.3
FLMB	39.3	40.5	36.7	46.7

($N = 5$). In addition, because these few samples were collected over a 3-mo period (late February–early May) encompassing the spawning season, the relative position in the spawning cycle of each collected bass in the sample may have varied significantly, potentially being responsible for much of the subspecific difference noted. In any case, the real issue is not fecundity advantage or disadvantage at the egg stage, but rather how many offspring recruit into the breeding pool, thus requiring the survival of offspring over at least one winter. As a result my study clearly shows that NLMB YOY are better adapted for recruitment in northern environments than FLMB, F_1, or F_x hybrid YOY.

The initial overproduction of FLMB in populations P-1 and P-2 was most likely due to the protracted spawning season in Illinois of FLMB compared to NLMB (Isely et al. 1987). Late-spawning FLMB found only their same subspecies with which to pair, and were apparently quite successful at producing large numbers of small, late-spawned offspring. The survival of these small FLMB over winter, however, was quite poor relative to NLMB and even to F_1 hybrids, confirming results from previous controlled experiments (Philipp and Whitt 1991). In fact, analysis of the genetic composition of the last year class studied in each of the experimental populations, P-1 and P-2, demonstrated that the overall contribution of the NLMB genome was greater than that of the FLMB genome (Table 10), 60.8% versus 39.2% (P-1) and 59.5% versus 40.5% (P-2). This increased contribution indicated that the relative fitness of the NLMB genome was greater than that of the FLMB genome. Even when experimental populations were initiated with 50% of original adults being F_1 hybrids (as in populations H-1 and H-2), the greater relative fitness of the NLMB genome over the FLMB genome was still evident, 63.3% versus 36.7% (H-1) and 53.3% versus 46.7% (H-2) for the overall genomic contribution to the last year-class studied (Table 10). However, introgression between the two genomes occurred very rapidly in both types of ponds, becoming almost if not totally complete after only 1–2 generations. The intergrade population that results (eventually all F_x individuals, each with some mixture of both the NLMB and FLMB genomes) has performance characteristics — survival and growth — that are less than the original NLMB population.

Isolated "trophy" catches in California after the introduction of "Florida strain largemouth bass" are responsible for much of the recent interest in propagating FLMB for introduction into waters outside of peninsular Florida. The largemouth bass populations in California prior to those introductions thirty years ago were themselves non-native, purportedly resulting from introductions at the turn of the century of NLMB, from Illinois. The relative suitability of these original introductions for the waters of southern California are certainly questionable. As a result, the apparent response of this introduced NLMB fishery to FLMB introductions may not at all reflect the response of native NLMB populations in the eastern half of the country to similar stocking programs.

Here I have shown that the result of mixing the two subspecies, NLMB and FLMB, is the production of an introgressed population composed of F_x hybrids. Philipp and Whitt (1991) have shown that in central Illinois FLMB, as well as both reciprocal F_1 hybrids, exhibit poorer growth than NLMB. Another controlled study (Williamson and Carmichael 1990) using pellet-fed, genetically-confirmed stocks of both subspecies and both reciprocal hybrids has been completed in Texas. The results of this study parallel our results, demonstrating that compared to FLMB, the NLMB showed significantly greater growth (first year) and lower mortality when exposed to low temperatures. Thus, there is no evidence to support the contention that the introduction of FLMB into NLMB populations in habitats such as those found in Illinois and Texas would create the "trophy" bass fishery intended. On the contrary, evidence suggests that the resulting population would have poorer growth characteristics than the original native NLMB population. So, even though Maceina et al. (1988) suggested that in Aquilla Lake, Texas FLMB females show a growth advantage over NLMB females after 3 yr of age, I feel that these conclusions are not warranted for several reasons. First, the results are only based on 12 fish collected throughout a 3-mo period during spawning. Second, the genetic history of these fish is questionable because of a lack of confirmation of the subspecific status of the hatchery stocks used to produce them. Finally, comparing NLMB and FLMB of all other ages in Lake Aquilla, these authors reported that FLMB were no larger than and often smaller than NLMB and F_1 and F_x hybrids. I certainly did not observe any "late blooming growth advantage" for FLMB or F_1 or F_x hybrids in Illinois. In addition, long-term studies in Texas (J. H. Williamson and G. J. Carmichael, pers. comm.) have also observed the opposite, a growth advantage for NLMB over FLMB, even after 7 yr.

Fisheries agencies should, indeed, strive to provide optimal opportunities for anglers. However, as the stewards over our dwindling natural resources, agencies must not risk the long-term health of native populations for short-term benefits that may or may not be realized. Since introduction programs that involve mixing stocks must be considered essentially irreversible actions, they should not be initiated until the results of extensive evaluation demonstrate unequivocally that the ensuing genetic alteration of recipient populations will not lead to their irreparable damage. Agencies that continue introduction programs involving these types of transfers simply to provide some presumptive benefit to anglers, now do so in the face of mounting evidence documenting the detrimental long-term consequences of those actions. The results I report here clearly suggest that programs involving the introduction of Florida largemouth bass into waters outside of peninsular Florida need to be reevaluated and, quite likely, terminated.

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Ecological and Genetic Effects of Salmonid Introductions in North America[1]

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Stocking of non-native Salmoninae into North American waters began around 1870. Brown trout (*Salmo trutta*) from Europe established populations across North America and is the only successful inter-continental introduction. Introductions of native salmonids within North America but outside their native ranges have been common. Ecological effects of salmonid introductions. include competition, predation on native salmonids and other fishes, environmental modification through digging of redds in stream bottom substrates during spawning, and introduction of parasites and disease to native fish. Direct genetic effects from stocked salmonids are caused by interbreeding with native species. Indirect genetic effects may result through selective forces and/or a reduction of effective population size, genetic drift, and inbreeding. Management actions used to remove non-native salmonid populations include chemical reclamation and construction of barriers to movement. Salmonid stocking as a management practice is appropriate for species or population rehabilitation. Continued stocking of non-native salmonids should cease where viable native salmonid populations exist. New introductions of Eurasian species should not be made because effects are unpredictable. Aquaculture and the creation of transgenic fish pose special threats to North American salmonids. The era of widespread, intentional introductions of salmonids by man justifiably is drawing to a close.

L'empoissonnement de certaines eaux d'Amérique du Nord avec des Salmoninae non indigènes a commencé aux environs de 1870. La truite brune, *Salmo trutta*, originaire d'Europe, dont on trouve des populations partout en Amérique du Nord, est le seul cas d'introduction intercontinentale fructueuse. L'introduction de Salmonidae indigènes, mais à l'extérieur de leur aire de distribution originale, a été courante. Parmi les effets écologiques de l'introduction de Salmonidae figurent la compétition, la prédation qui s'exerce sur des Salmonidae indigènes et d'autres espèces de poissons, les modifications environnementales attribuables au creusement de nids pendant le frai à même les matériaux formant le lit des cours d'eau et l'introduction de parasites et de maladies attaquant les espèces indigènes. Les effets génétiques directs de l'empoissonnement avec des Salmonidae résultent de la reproduction croisée avec des espèces indigènes. Les effets génétiques indirects peuvent être attribuables à des forces de sélection ou à une réduction de la taille effective d'une population, à une dérive génétique et à des croisements consanguins. Les méthodes de gestion utilisées pour éliminer les Salmonidae non indigènes comprennent l'ajout de produits chimiques pour désempoissonner des plans d'eau et la construction de barrières limitant les déplacements. L'empoissonnement avec des Salmonidae est une pratique de gestion qui convient au rétablissement d'espèces ou de populations. L'empoissonnement continuel avec des Salmonidae non indigènes devrait être interrompu là où il existe des populations de Salmonidae viables. On ne devrait pas procéder à une nouvelle introduction d'espèces eurasiennes, car les effets sont imprévisibles. L'aquiculture et la création de poissons transgéniques constituent une menace particulière pour les Salmonidae d'Amérique du Nord. L'époque où l'homme pouvait justifier l'introduction intentionnelle et généralisée de Salmonidae tire à sa fin.

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Widespread introductions of trout and salmon in North America began around 1870 and were common by the turn of the century. The initiation of these stocking programs corresponded with major advancements in fish cultural practices, especially the artificial fertilization and hatching of salmonids, and the construction of rapid transportation systems, most notably railroads (Bowen 1970; Moyle 1986). By the 1960's, fish cultural technology had advanced to the point that salmonid hatcheries capable of producing millions of fish annually were being used to stock bodies of water as large as the Great Lakes (Parsons 1973). Over this time period from 1870 to 1970, a variety of North American and European salmonid species were introduced outside of their native ranges. For example, 10 exotic species of Salmoninae were introduced into Michigan waters between 1873 and 1972 (Latta 1974).

The term, introduction, is used here to mean transfers of fish by man, sometimes repeatedly, into waters outside of their native ranges. Introductions may be categorized into three types based on origins of the fish used: inter-continental transfers, the stocking of native species within North America but outside of their native ranges (intracontinental transfers), and the transfer of genetically differentiated stocks within native ranges (stock transfers). Successful introductions result in the sustained

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naturalization of species or stocks in their new environment. Most introductions have occurred by intentional or purposeful actions to "improve" native fish communities for humans (Courtenay and Kohler 1986). Only rarely have successful introductions of salmonids occurred from the accidental release or escape of fish.

The introduction of salmonid species has had a profound and permanent effect on the native fish fauna of North America. These effects may be classified as ecological or genetic. Ecological effects involve processes or mechanisms such as competition, predation, and habitat alteration (Taylor et al. 1984; Moyle et al. 1986), and are a direct consequence of the genetic character of the species introduced. Genetic effects involve processes which change the gene pools of populations and species. Ecological and genetic effects, in theory, may cause native species to (1) be eliminated, (2) have changes in growth and survival, (3) be genetically changed, (4) alter community structure, (5) exhibit combinations of the above, or (6) exhibit no detectable changes (adapted from Moyle et al. 1986). Typically, the effects of introductions have been discussed in terms of the impacts of one species on another. However, important intraspecific effects may also result from the introduction of stocks or populations that are genetically differentiated from native populations of the same species (i.e., stock transfers; Krueger et al. 1981).

The purpose of this paper is to provide a review of trout and salmon (Salmonidae: Salmoninae) introductions in North America, and to examine the evidence for ecological and genetic effects of these introductions. The primary focus will be on effects that have occurred between introduced and native salmonids. Interactions between introduced salmonids and other native fishes and other aquatic organisms such as invertebrates will be discussed minimally. The effects that have occurred on fisheries from the introduction of salmonids will not be discussed (e.g., Hansen et al. 1990).

Review of Salmonid Introductions

The stocking and subsequent naturalization of non-native salmonids has occurred worldwide on all continents except Antarctica. Notably successful introductions have occurred with the North American salmonids, especially the brook trout (*Salvelinus fontinalis*) and rainbow trout (*Oncorhynchus mykiss*), to Europe, South America, Africa, and Asia (MacCrimmon and Campbell 1969; MacCrimmon 1971)). In contrast, the only successful inter-continental transfer of a salmonid species to North American waters has been the brown trout (*Salmo trutta*) from Europe (Luton 1985). Salmonid species that have been introduced to North America but failed to establish populations include the cherry salmon (*O. masou*; Christie 1970), the Ohrid trout (*Salmo letnica*; Courtenay et al. 1984), and the Danube salmon or huchen (*Hucho hucho*; Crossman 1984).

Although few inter-continental transfers of salmonids have been made into North American waters, intracontinental introductions of native salmonids to areas outside their natural distribution have been extensive. Such introductions have occurred for virtually all North American species of *Oncorhynchus*, *Salmo*, and *Salvelinus* at one time or another. Salmonids from Pacific drainages that have established populations outside of their original ranges include: rainbow trout into the Great Lakes drainages (MacCrimmon and Gots 1972) and other Atlantic drainages from the Appalachian Mountains to Newfoundland (King 1937; King 1942; Chadwick and Bruce 1981; Whoriskey et al. 1981; Moore et al. 1983), golden trout (*O. aquabonita*) from the Kern River drainage in California into the high mountain lakes of the Sierra Nevada and mid-continent Rocky Mountains region including Alberta (Crossman 1984), the chinook, coho, and kokanee salmon, (*O. tshawytscha, O. kisutch, O. nerka*) into the Great Lakes/St. Lawrence River and other Atlantic drainages (Parsons 1973; Stolte 1974; Symons and Martin 1978; Withler 1982; Martin and Dadswell 1983; Emery 1985; Dumont et al. 1988), and the kokanee salmon into lakes and reservoirs throughout the west (Wydoski and Bennett 1981).

Similarly, salmonids from eastern North America (Atlantic coast to the Mississippi drainage and north) have been introduced westward. Most notable has been the naturalization of brook trout to waters from the Rocky Mountains west to the Pacific Ocean. Lake trout (*Salvelinus namaycush*) have also established populations in western North American lakes such as Lake Tahoe, Nevada and Lewis Lake, Wyoming, but naturalized populations of this species are less widespread outside its range than the brook trout. The Atlantic salmon (*Salmo salar*) has been stocked into the upper Great Lakes (Parsons 1973) westward to the Pacific drainages such as Cowichan Lake, British Columbia (introductions included salmon of North American and Scottish origins, Crossman 1984). Although establishment of Atlantic salmon populations has not occurred, their presence in lakes has been maintained by annual stocking. Species such as Dolly Varden trout (*Salvelinus malma*) and Arctic char (*S. alpinus*) have not been a part of the extensive stocking programs focussed on other North American salmonids. In the west, many lakes above 1 500–2 000 m were originally barren of fish but now contain introduced populations of salmonids from eastern and western North American sources (brook, brown, rainbow, cutthroat, and golden trout; Moyle 1986).

The transfer of stocks or populations of species within native ranges has been both extensive and poorly documented. Stock transfers have probably been the most common type of introduction to occur in North America because stocking programs have been an important part of management conducted by fishery agencies. The extensive nature of these introductions can be illustrated by a genetic study of brook trout initiated by the authors and D. Perkins. This project required the sampling of brook trout populations from the waters of the Adirondack Mountain region of New York where stock transfers had not occurred. Fewer than 25 (2.3%) out of 1 100 brook trout lakes and ponds in the Adirondack region were identified as unstocked based on historic records. Species restoration programs such as those conducted for lake trout and Atlantic salmon have often used stock transfers as a management action. For example, lake trout from Clearwater Lake, Manitoba have been stocked regularly into Lake Ontario for more than 10 yr (Krueger et al. 1989). In some cases, the stocks transferred are recognized subspecies. For example, Yellowstone coutthroat trout (*Salmo clarki lewisi*) have been stocked for more than 35 yr into Glacier National Park waters that contained westslope cutthroat trout (*S. c. bouvieri*; Marnell 1988).

Inter-continental stock transfers have been rare because few species are native to more than one continent. Clearly the potential exists for species such as Arctic char, Atlantic salmon, and those in the genus *Oncorhynchus* to be introduced from other continents. As mentioned above, Atlantic salmon from European origins have been stocked in North America. In addition, Arctic char from France were released into Westward Lake,

Ontario and three lakes in Saskatchewan; however, these lakes did not originally contain char (Crossman 1984).

The stocking of hybrids between species has been much less common than the transfer of species or stocks. The most extensive hybrid stocking program has been one administered by the Province of Ontario as part of a fishery rehabilitation project for Lake Huron (Berst et al. 1980). Splake, the fertile hybrid between lake and brook trout, were first stocked in the 1950's as a replacement for the lake trout which was nearly extinct as a result of sea lamprey predation. Later in 1969, splake selected for early maturity and retention of swimbladder gas were begun to be stocked, as were backcrosses between selected splake males and female lake trout. Although a substantial amount of natural recruitment has not been observed, natural spawning of these hybrids has occurred in Lake Huron. Splake have also been stocked into Precambrian Shield lakes of Ontario and lakes of Alberta. A self-reproducing stock was established in Lake 17, Ontario after an initial planting of 5 460 F_1 hybrids (Berst et al. 1980). In 1951, Agnes Lake, Alberta was stocked with 1 000 F_1 splake. Natural reproduction was first confirmed in 1955 and has continued at least through 1967 (Goldberg et al. 1967).

In most cases, introductions of salmonids have been intentional as part of stocking programs intended to "enhance" aquatic communities for fishing. In some instances, remarkable sport fisheries have resulted from these stocking programs such as for Pacific salmon in the Great Lakes (Hansen et al. 1990). Enhancement or supplementation programs to benefit commercial fisheries for anadromous species have also been successful. For example, sockeye salmon (*O. nerka*) have been stocked extensively in Pacific drainages and expanded the range for this species (e.g., Blackett 1979). Stock transfers for this purpose may be increasing along the Pacific coast (Helle 1981). A notable exception to intentional stocking was the accidental introduction and subsequent wide-spread establishment of the pink salmon (*O. gorbuscha*) from the Pacific Ocean to Lake Superior and their subsequent spread downstream to other Great Lakes and Atlantic drainages (Emery 1981; Kwain and Lawrie 1981; Randall 1984). Escapement from pen-rearing aquaculture operations (e.g., Atlantic salmon along the Pacific coast) will likely serve as a new source of introductions in the future.

Ecological Effects of Salmonid Introductions

Competition

Salmonids introduced into lakes and streams may compete with native fish faunas for food and space. Competition here refers either to the use of resources that are in short or inadequate supply with respect to the potential demand (exploitation competition) or to the use of a resource by a species that interferes with the use of that resource by another species regardless of supply (interference competition). Competitive interactions may lead to (1) the extinction of one species, (2) fluctuating coexistence as the environment alternately favors one species then the other, and (3) niche shifts (Moyle and Vondracek 1985). Competition in streams may occur as species attempt to secure territories for adequate space and, therefore, food and cover (Chapman 1966). Interspecific competition may be most intense during late summer in years of high population abundance when stream flows are often low, and space and food are minimal (Griffith 1988). Under other circumstances, stream populations of salmonids may be more likely regulated through climatic factors such as droughts, floods, or severe winters. Competition between species may be more intense in lakes than in streams because climatic factors are presumed to be less effective regulators of fish populations. This increase, however, may be balanced by reduced territorial behavior in lake habitats because of the increased spatial dimensions and an absence of current (Griffith 1988).

Competition is the most commonly invoked process used to explain the ecological effects of salmonid introductions. For example, native brook trout have disappeared from many waters in eastern North America, especially streams, over the past 100 yr and have been replaced by the recently naturalized, European brook trout. Competition between the species has often been suggested as the process that caused the species shift. Both species occupy similar stream habitats and appear to have considerable diet overlap (e.g., Metzelaar 1929; Nyman 1970; Johnson 1981). In one study, brown trout dominated and excluded brook trout from preferred resting positions in streams during the summer which may reflect a form of interference competition between these species (Fausch and White 1981). Studies of winter habitat preferences have also indicated considerable overlap between the two species; however, interaction at this time of year may be reduced by the lack of agonistic behavior at low temperatures (Cunjak and Power 1986). Competition for space and food in a fluctuating stream environment has been offered as a partial explanation for the replacement of brook trout by brown trout in a Minnesota stream over a 15-yr time period (Waters 1983). Competitive advantages of brown over brook trout may have been enhanced by widespread changes in habitat that have occurred in this region (e.g., deforestation and summer warming of streams).

In other streams of eastern North America, the brook trout has been replaced by rainbow trout introduced from Pacific drainages. These streams have headwater regions that contain only brook trout, followed by a middle zone of sympatry between rainbow and brook trout, and downstream sections dominated by rainbow trout. As with the brown trout, competition between the species often has been suspected as the cause of the displacement of brook trout. However, the potential competitive advantages of rainbow trout over brook trout often have been unclear. For example, brook trout seemed to dominate rainbow trout in environments of low water velocity and temperature (13°C), while no advantage for either species occurred in high water velocity and temperature (19°C; Cunjak and Green 1983, 1984, 1986; see discussion by Fausch 1988). In contrast, Gibson (1981) reported, based on experimental observation, that rainbow trout were more aggressive and could displace brook trout from preferred stream areas. Cunjak and Green (1983) suggested habitat segregation between brook and rainbow trout may be a function, in part, of competitive interactions; however, Fausch (1988) has aruged that their data better support the conclusion that genetically fixed differences in fundamental niche may exit between these species that minimize competitive interaction. Several studies also have been conducted over many years on sympatric populations of brook and rainbow trout in Sagehen Creek, California (Gard 1961; Gard and Seegrist 1972; Seegrist and Gard 1972; Gard and Flittner 1974; Erman 1986). Population abundance of these species has fluctuated considerably over time in this stream. Though competition may have played a role in the dynamics of the trout populations, the effects of beavers (*Castor canadensis*) on habitat, and floods and droughts on recruitment processes, may have been more important factors (see

discussion by Fausch 1988). The lack of consistency between studies may be related to the difficulties inherent in extrapolating laboratory studies to field observations. Recent studies focused in the Appalachian Mountains and the Great Lakes offer better resolution of the interaction between these two species.

The disappearance of brook trout from streams of the southern Appalachian Mountains may have been caused by competition with naturalized rainbow trout (King 1937; Larson and Moore 1985). Growth rates of both species have been observed to be about equal until spring of the second year of life when rainbow trout gain a growth advantage over brook trout (Whitworth and Strange 1983). This advantage results in a larger size-at-age rainbow trout over brook trout that then continues for the rest of their lives. Also, rainbow trout appear better able than brook trout to occupy the shallow riffles and pools that characterize this region's streams (Larson and Moore 1985). These authors observed that brook trout shifted to unfavorable positions away from main currents when rainbow trout were abundant. The shift in position by brook trout, presumably away from optimal feeding stations, could be the source, or may contribute to, the growth rate differences observed between the species. The size advantage that rainbow trout gain as a a result should further enhance the ability of this species to occupy preferred positions in streams. In another study in four Appalachian streams, rainbow trout population densities were reduced an average of 88% by electrofishing (no. 100 m^{-2}). In response, brook trout standing stocks (kg ha^{-1}) substantially increased in all four streams over a 6-yr period and did not follow the changes in density observed in three allopatric control sections (Moore et al. 1983; Moore et al. 1986). These field studies provide some of the best evidence available for competition between rainbow and brook trout (see review by Fausch 1988); although, processes such as predation in addition to competition could also have contributed to their outcomes.

In some Lake Superior tributaries, brook trout are abundant upstream from waterfalls that prevent access to spawning, non-native rainbow trout from the lake. Downstream from these falls, rainbow trout juveniles are typically more abundant than brook trout. In a study conducted on a Lake Superior tributary, growth of young-of-the-year brook trout was significantly suppressed after emergence of rainbow trout fry in June (Rose 1986). Exploitative and interference competition between rainbow and brook trout for invertebrate foods was suggested as a likely cause for the results. Competition by the rainbow trout may explain part of the reason for the displacement of brook trout in this region. Brook trout populations in Great Lakes tributaries may also be threatened by competition for food and space from recently introduced coho salmon which emerge earlier, are larger, and have similar habitat preferences as brook trout juveniles (Fausch and White 1986; Gibson 1981).

Many cutthroat trout populations declined precipitously in western North America after non-native salmonids were introduced about 100 yr ago. Competition has often been inferred as the mechanism that caused displacement of cutthroat trout by non-natives; however, changes in habitat and fishing pressures often have contributed to these declines as well (see review by Griffith 1988). Few studies have been conducted to identify the competitive mechanisms involved between cutthroat trout and non-native species. In Yellowstone National Park, the introduction of the brook trout has nearly always resulted in the disappearance of Yellowstone cutthroat trout (Varley and Gresswell 1988). Similarly, brook trout displaced Lahontan cutthroat trout between 1960–70 in Pole Creek, a tributary to the Truckee River, California (Gerstung 1988). The larger size of brook trout over cutthroat trout of similar age may confer a competitive advantage. In northern Idaho streams, brook trout maintained a 20 mm size advantage over cutthroat trout of the same age groups due to their earlier emergence (Griffith 1972). Introduced rainbow, brown, and lake trout have also displaced cutthroat trout at many locations; however, mechanisms that caused the disappearance of cutthroat trout are conjectural (Moyle and Vondracek 1985; Gerstung 1988). For example, cutthroat trout disappeared from the Henrys Fork of the Snake River, Idaho within 8 yr after the introduction of rainbow trout (Griffith 1988). Rainbow trout may have a competitive advantage over cutthroat trout because they appear to be more aggressive than equal-sized cutthroats (Nilsson and Northcote 1981). Kokanee salmon introduced in lakes may also compete with cutthroat trout for plankton food (Gerstung 1988; Marnell 1988).

The golden trout has also suffered from introductions of non-native salmonids presumably through competition. This species was originally endemic to the Kern River watershed in the eastern Sierra Nevada Mountains of California (Schreck and Behnke 1971). Introduced brown, brook, and rainbow trout have displaced golden trout, possibly through competitive mechanisms (Pister 1991). The brown trout, in particular, appeared to successfully defend territories and out-compete golden trout for space in the upper South Fork of the Kern River (Pister, E. P., California Department of Fish and Game, personal communication).

Predation

Predation by introduced salmonids on native salmonids or other aquatic organisms has been little studied in North America. A few references exist, often without details, that note predation by non-native salmonids. For example, lake trout introduced to lakes in Glacier National Park may be a significant cause of mortality of native westslope cutthroat trout through predation (Marnell 1988). Introduced chinook and coho salmon in the Great Lakes also have been noted for their predatory effect on alewife (*Alosa pseudoharengus*, Stewart et al. 1981).

European brown trout are known to be piscivorous and feed upon native brook trout. For example, stomachs of brown trout larger than 30 cm from the North Branch of the Au Sable River, Michigan were found to contain high proportions of fish, notably brook trout (Alexander 1977). A significant increase in brook trout larger than 22.9 cm occurred when 40–66% of brown trout of this size were removed and American mergansers (*Mergus merganser*) were harassed and chased from a section of this river (Shetter and Alexander 1970). Brown trout were also suspected to be an important predator of golden trout in the Upper Kern River drainage in California (Pister, E. P., California Department of Fish and Game, personal communication).

The effects of introduced salmonids on non-salmonid fishes have been rarely investigated. In a Virginia stream, large (>28 cm) and small (<28 cm) brown trout were experimentally stocked in the spring and changes in the fish community were monitored over the summer and fall (Garman and Nielsen 1982). While small brown trout rarely ate fish, large trout ate five species of fish consistently through the study period of May–November. Abundance of the major prey species, the tor-

rent sucker (*Moxostoma rhothoecum*), decreased in the section stocked with large trout but remained constant over the same time period in a reference section. Similarly, predation by brown trout on a threatened native sucker species (*Catostomus microps*) from northern California may be a mechanism that affects abundance of the sucker population (Moyle and Marciochi 1975). We conclude, based on these studies, that large brown trout can alter the abundance of native fish fauna in North American waters through predation.

Introduced non-native salmonids may also feed upon and affect the abundance of native invertebrates and amphibians. The disappearance of three pelagic cladoceran species of zooplankton in Lake Tahoe has been attributed, in part, to predation by naturalized kokanee salmon (Morgan et al. 1978). Introduced salmonids are also known to feed on benthic invertebrate populations (e.g., Wurtsbaugh et al. 1975), but little documentation of the effects of predation on abundance and distribution of invertebrates has occurred. Such effects may be important, especially in barren lakes. For example, four species of trout and salmon introduced over many years into fishless mountain lakes in California were reported to have altered native invertebrate and amphibian populations (Herbold and Moyle 1986).

Environmental Modification

Some introduced fishes can modify their environments through feeding and other activities and adversely affect native fishes. The common carp (*Cyprinus carpio*) and the grass carp (*Ctenopharyngodon idella*) are well-known examples of non-salmonid introduced fishes that can remarkably alter their aquatic environments. These fish can cause a reduction in aquatic macrophytes and an increase in turbidity often to the detriment of native fishes (Taylor et al. 1984). Similar types of environmental effects from introduced salmonids seem unlikely due to the behavioral patterns characteristic of this family. However, salmonids that spawn in streams do modify their habitat by digging redds in the stream bottom for incubation of their eggs. In streams, population size can be regulated by habitat variables, such as the availability of spawning gravels and juvenile rearing space, that affect recruitment to the next generation. As a result, the number of spawners each year will tend to be in some form of equilibrium with the available spawning habitat. Stocking of salmonids can decouple the feedback mechanisms that naturally control spawner density and result in unusually large numbers of spawners using the available habitat. By their digging activities, these fish could significantly reduce invertebrate production by dislodgement or destruction, disturb redds of native salmonids that spawn at the same time of year, or disrupt habitat for fish species such as sculpins (*Cottus* sp.). The massive stocking of coho and chinook salmon in the Great Lakes has often resulted in exceptionally large spawning runs of salmon up rivers in the fall. In the Platte River, a Lake Michigan tributary, invertebrate populations of 12 taxa decreased significantly in terms of number and weight m^{-2} after the spawning of introduced coho salmon (Hildebrand 1971). As a result, food supplies for native fishes in this region could be affected negatively through the spawning activities of introduced salmon. The possibility also exists that Pacific salmon from the Great Lakes, through modification of spawning habitats, could physically destroy eggs of native brook trout which are deposited at about the same time in the fall.

Introduction of Parasites and Disease

Stocking of non-native salmonids may result in the inadvertent introduction of parasites and pathogens to indigenous salmonid populations. Disease transmission to wild fish populations may also occur from fish that escape from pen-rearing operations used in commercial aquaculture (Barinaga 1990). If a native population has little natural immunity or resistance to a disease, the results of infection can be disastrous to the population. Stocking of Atlantic salmon smolts from Sweden in 1975 likely caused the introduction of a parasitic fluke (*Gyrodactylus salaris*) to wild populations in Norway (Johnsen and Jensen 1986; Sattaur 1988). Since the initial introduction, the distribution of the parasite in 26 infected rivers has been closely associated with stocking from six infected Norwegian hatcheries (Johnsen and Jensen 1986). In these rivers, a dramatic reduction of populations of salmon parr has occurred and catches of adults in later years have sharply declined. The existence of all wild Atlantic salmon populations in Norway is now considered threatened by this parasite (Hindar et al. 1991).

Documentation of disease introductions in North America from the stocking or escape of salmonids has been uncommon. Dumont et al. (1988) cites a report of infectious pancreatic necrosis in non-native coho salmon in Lake Ontario but not its transmission to native salmonids. In Wyoming, bacterial kidney disease (BKD) has been transmitted from stocked infected hatchery trout to naturalized non-native brook, brown, and rainbow trout populations (Mitchum et al. 1979). Whirling disease, caused by the protozoan, *Myxosoma cerebralis*, was introduced from Europe to North America from a shipment of frozen rainbow trout (see reviews by Hoffman and Schubert 1984 and Marnell 1986). The disease has been found to be pathogenic to rainbow and brook trout in North America. A wild brook trout population in Michigan has been reported to be infected with whirling disease downstream from an infected hatchery (Yoder 1972).

Diseases have been introduced from North America to other locations through transfers of salmonids. For example, infectious hematopoietic necrosis virus (IHNV) was introduced from Alaska through a shipment of sockeye salmon eggs to a hatchery in Hokaido, Japan (Rohovec et al. 1988). The disease subsequently spread to cultured and wild populations throughout the country.

Release or escape of diseased fish from hatcheries or aquacultural operations does not always result in an epidemic among wild fish or detectable transmission of the disease to the wild. In two studies that used experimental stockings of infected hatchery brook trout, BKD and furunculosis were minimally transmitted to wild resident brook trout (Allison 1961; McDermott and Berst 1968). Similarly, the stocking of brook trout, that were carriers of infectious pancreatic necrosis virus, into an Alberta lake resulted in little transmission of the disease into other salmonids present (Yamamoto and Kilistoff 1979). Hatchery water, after being used for rearing BKD infected Atlantic salmon, did not readily infect wild salmon when discharged into the Margaree River, New Brunswick (Pippy 1969). Lack of disease transmission was certainly a fortunate outcome of these studies.

Development of disease control programs among management agencies has been encouraged to reduce the risk of disease introduction from infected fish destined for stocking (Goede 1986). Concern about disease transmission from introduced salmonids, especially from Pacific drainages, has been an impor-

tant consideration in the development of a fish disease control policy in the Great Lakes (Meyer et al. 1983; Hnath 1991; Horner and Eshenroder 1991). The basin-wide policy was developed by representatives from state, provincial, and federal agencies and from private aquaculture interests and coordinated by the Great Lakes Fishery Commission. The policy requires agency members to prepare a justification and proposal six months prior to importation and to secure consensus approval. The policy also establishes conditions for importation, including the need for quarantine. Policies and regulations to control movement of fish and fish eggs to prevent the spread of disease have been developed among several other organizations such as the Food and Agriculture Organization of the United Nations, Title 50 of the U.S., and the Pacific Northwest Fish Health Protection Committee (Rohovec et al. 1988). The development of these policies and regulations, in general, represents a widespread agreement among fish managers of the dangers inherent from disease transmission by the importation and transplantation of non-native fish.

Genetic Effects of Salmonid Introductions

The genetic effects of introductions of exotic species are defined as alterations in the gene pools of indigenous species. These alterations may be direct as in introgression (gene flow) or indirect such as a reduction of effective population size making native populations vulnerable to the effects of genetic drift and inbreeding. The decline in population numbers in this latter case may be caused by the ecological processes described earlier. Direct genetic effects include crosses between species leading to sterile hybrids (e.g., the tiger trout, a hybrid between introduced brown and native brook trout), crosses between species leading to introgression of the introduced species' genes into the gene pool of the native species (e.g., rainbow trout × cutthroat trout), and intraspecific or interstock crossing leading to gene flow into indigenous populations (e.g., stocking of hatchery reared fish into a stream with a native wild population; see Campton 1987).

Direct Genetic Effects

Infertile interspecific hybrids

While most definitions of species include some form of reproductive isolation, often this isolation has been geographic or behavioral. The introduction of an exotic species removes the effectiveness of geographic barriers and may also alter behavioral isolating mechanisms. Once hybridization takes place other forms of reproductive isolation may occur, such as infertility.

Interspecific hybridization has been observed in the wild between native and introduced species. The stocking of brown trout has led to reports of tiger trout hybrids from waters in Ontario (Whitzel 1983), Montana (Brown 1966), and Alberta (Allan 1977). Also, the hybrid between brown trout and native Atlantic salmon has been reported from a Nova Scotia river (Beland et al. 1981). As described earlier, the hybrid between lake and brook trout (splake) is fertile and has established populations in Canada after hatchery introduction. Hybridization occasionally does occur even among native species, for example, between anadromous rainbow and cutthroat trout (Campton and Utter 1985) and between chinook and coho salmon (Barley and Gall 1990). Most diploid crosses of salmonid species produce no hybrids or produce weak individuals without the survival qualities of either species. The existence of these naturally occurring, typically infertile F_1 hybrids is rare and short lived (no future generations), and therefore the ecological effects from their presence in fish communities is probably minimal. However, artificial techniques are now available to produce large quantities of viable but infertile triploid interspecies hybrids (see Thorgaard 1983). Triploid hybrids may pose a more serious threat to native salmonids and could cause important ecological effects or indirect genetic effects if stocked.

Interspecific introgression

Introgression is the flow of genes from one species gene pool into the gene pool of another species (or subspecies). Frequently, genes are transmitted through introgression to both species (or subspecies) if a narrow contact zone occurs between their geographical distributions. If only a small amount (<0.1%) of gene flow occurs, introgression may be viewed as increasing the capability for adaptation because the process introduces new variation upon which natural selection can operate. A larger amount of gene flow may disrupt the adaptive gene complexes which have evolved over time to permit the native species to effectively use its particular environmental niche. The ultimate threat of introgression is that the flow of genes never stops, and that eventually one gene pool is effectively replaced by that of the other species (or subspecies). Even if the flow of genes is stopped, the effects of introgression may be significant over evolutionary time scales.

Introgression from introduced salmonids has played and continues to play a role in the evolution of native salmonid gene pools, especially in western North America. The principal recipient native species in this region have been the golden trout and various subspecies of cutthroat trout. The principal donor species has been the ubiquitously introduced rainbow trout. Documentation of introgression is much easier in this case than for intraspecific gene flow (between stocks or populations) since the degree of genetic divergence is greater at the species or subspecific level than typically occurs among populations. For example, introgression between the introduced rainbow and native golden trout in California has been reported from field observations of morphological characters (Schreck and Behnke 1971; Moyle 1976). Based on allozyme analysis, introgressive hybridization has been documented between the introduced rainbow trout and native Paiute cutthroat trout of California (*S. c. seleniris*, Busack and Gall 1981). Introgression with rainbow trout has also been detected in native cutthroat populations located in Montana (8 of 16 samples from the Yellowstone River drainage) and Utah (7 of 39 samples) based on allozyme analysis (Allendorf and Leary 1988; Martin et al. 1985). Analyses of mtDNA coupled with allozyme variability has readily permitted the estimation of the degree of introgression among subspecies of cutthroat trout. For example, Gyllensten et al. (1985) have shown that cutthroat trout in Forest Lake, Montana represented a hybrid swarm of native westslope (*S. clarki lewisi*) and introduced Yellowstone (*S. c. bouvieri*) cutthroat trout based on mtDNA and allozyme analyses. Gene flow through introgression has occurred to both subspecies gene pools and breeding has been essentially random. This population now no longer represents either subspecies, but will continue to evolve into a new subspecies as long as it remains isolated from other populations. Similar evidence for introgression between native and introduced subspecies of cutthroat trout has been reported for other populations in Montana (Marnell et al. 1987; Allendorf and Leary 1988).

Intraspecific gene flow

By far the most difficult category of genetic effects to document are those that involve different populations of the same species. The difficulty in documentation occurs because the parentage of progeny from interstock matings usually are unrecognizable morphologically and biochemically. However, this type of genetic effect may be common because stocking programs have been a common and widespread practice of fishery management throughout North America.

Interbreeding between introduced and native populations will result in a reduction of genetic variability between the populations (a ''homogenizing'' effect) and outbreeding depression. Populations evolve to maximize their fit to the ecological niche which they occupy. Such evolution leads to changes in the gene pool of a population that cause it to be suited to a particular environment. If a source of fish, genetically different from the population in the receiving waters, is introduced and successfully breeds with the resident fish, genetic differences between the populations will decline. If the stocking program is widespread and interbreeding frequent, locally adapted native stocks will be replaced by larger more homogeneous populations (Allendorf and Leary 1988). Outbreeding depression will be a consequence caused by interbreeding of populations and will result in a decline in fitness (their capability to reproduce new generations). Initially the F_1 generation may exhibit increased fitness as coadapted gene complexes from both parents remain intact and may provide substantial benefit to the progeny (heterosis or hybrid vigor). However, recombination in later generations (F_2 and beyond) will disrupt these gene combinations and cause fitness to be lower than either parental population. The genetic danger to native salmonids from outbreeding depression is substantial; however, few studies have documented its occurrence as a result of interbreeding between hatchery and wild salmonids (Gharrett and Smoker 1991).

Most fishery management agencies practice some form of fish population enhancement via stocking. In many cases this activity involves planting of young fish, progeny of hatchery broodstocks, into streams or lakes that have naturally reproducing populations. The hatchery strain typically bears little genetic similarity to the wild population except as members of the same species (see review by Allendorf and Ryman 1987). The genetic differences between hatchery and wild fish often translate into important differences in physiological, behavioral, and other traits related to fitness (e.g., Reisenbichler and McIntyre 1977; Swain and Riddell 1990; Johnsson and Abrahams 1991). Stocked strains often have a long, undocumented history in a hatchery system and have been derived from fish of various geographic origins (e.g., the McCloud River hatchery strain of rainbow trout used in many hatchery programs; Needham and Behnke 1962). In some cases the introduced stock represents an outcross of a hatchery strain to a widely divergent gene pool in order to maximize first generation heterozygosity and potential hybrid vigor (Flick and Webster 1976). This practice, however, does not take into account the subsequent breakdown of hybrid vigor in later generations as described earlier (outbreeding depression).

While extensive documentation exists regarding the success of plantings as measured by catch records (e.g., Lachance and Magnan 1990), the genetic contribution of these fish to the next generation is usually unknown (see Chilcote et al. 1986; Marsden et al. 1989). In order to detect this second generation effect one needs to be able to examine genetic characters that distinguish populations and are transmitted to subsequent generations. Interbreeding has been documented between native and introduced populations of rainbow trout in the Yakima River of Washington based on allozyme data (Campton and Johnston 1985). Similar results were shown for a population of rainbow trout in the Kootenai River drainage of western Montana (Allendorf et al. 1980). A loss of inter-populational genetic diversity appears to have occurred among rainbow trout (steelhead) populations of the Olympic Peninsula, Washington as a result of hatchery stocking since the 1940's (Reisenbichler and Phelps 1989). Genetic differences among Olympic Peninsula populations were much less than those observed among populations in British Columbia where little stocking has occurred (Parkinson 1984). A similar reduction in gene diversity may have occurred among chinook salmon populations of the lower Columbia River which have experienced an extensive history of stocking (Simon 1972; Utter et al. 1989).

Some studies have not found evidence for interbreeding and gene flow between hatchery and wild fish. For example, native populations of rainbow trout in southwestern Idaho (Wishard et al. 1984) and brook trout in Wisconsin (Krueger and Menzel 1979) appeared not to have experienced gene flow with stocked fish. In an extensive survey of 86 populations of chinook salmon from British Columbia to California, the distribution of genetic variation was associated with probable historic routes of recolonization after glaciation even though massive stockings of salmon have occurred recently in some regions (Utter et al. 1989). If interbreeding between hatchery and wild chinook salmon was common these historic relationships should have been disrupted. Lack of evidence for interbreeding between hatchery and wild salmonids for the reasons that follow (adapted from Steward and Bjornn 1990):

- *interbreeding and gene flow has not occurred or been extensive because of poor survival or other life history or genetic mechanisms effectively blocking spawning success of hatchery fish.
- *effects of gene flow cannot be distinguished from changes caused by natural selection or genetic drift.
- *available technology is inadequate to discern the extent of gene flow that has occurred.
- *genetic differences between hatchery and wild stocks may be small; hatchery practices may not have altered historic genetic compositions in the comparatively short time that hatchery fish have been cultured.

As a result, a lack of evidence for interbreeding and gene flow can lead to several alternative explanations, only one of which is that it has not occurred.

Indirect Genetic Effects

The introduction of a non-native salmonid may cause one or more indigenous species or populations to decline in numbers or range such that their gene pool is changed. Reductions in effective population size increase rates of genetic drift and inbreeding which can produce changes in allelic frequencies. These changes may occur as random increases in unfavorable alleles which could reduce the overall genetic adaptability of the population (or species). A reduction in fitness may contribute to ecological processes such as competitive displacement and result in the ultimate extinction of the species or population. Reductions in native range will undoubtedly lead to reductions in the overall genetic variability of the species, without necessarily leading to changes in the individual gene pools of the remaining populations.

Indirect genetic effects have probably occurred in native populations of brook trout in the Appalachian Mountains, where populations have declined sharply over the past 60 yr due to introductions of rainbow trout (discussed earlier). Gene flow is now substantially reduced, if not prevented, between these remnant populations in this region which are confined to only the headwater areas of streams. These populations are important because they probably represent a geographically restricted, separate subspecies of brook trout (Stoneking et al. 1981). The end result of the displacement of brook trout in this region is that the overall gene pool of brook trout has been significantly reduced and that the remaining populations have reduced numbers and are disjunct from one another. A similar situation exists for many of the native cutthroat trout populations in western North America.

A second type of indirect genetic effect is an alteration of selective forces caused by introduced salmonids in the environment (Krueger and Menzel 1979). New forms of competition, predation, environmental modification, and parasites and disease caused by non-native salmonids each may contribute to a modification of selection pressures. If selective pressures are modified, native fish gene pools must evolve in order for the populations or species to survive. Documentation of the nature and extent of this type of genetic effects is difficult to prove and remains as a challenge to future investigations.

Management of Unwanted Salmonid Introductions

Management actions used to reverse or prevent the negative effects of salmonid introductions have included population reduction through massive chemical reclamation and the construction of barriers to fish movement. Less than total eradication of an introduced species may be inadequate to reduce interactions with native fish to the level desired. For example, although removal of approximately 60% of the large brown trout in a Michigan river appeared to cause an increase in brook trout, the investigators concluded that brown trout would have to be reduced to considerably lower levels to improve the sport fishery (Shetter and Alexander 1970).

Total eradication of non-native salmonids has occurred in some instances. Concern over the competitive interactions between introduced brook trout (discovered in 1985) and native cutthroat trout in Arnica Creek, a direct tributary to Yellowstone Lake, resulted in a chemical treatment to remove all fish (Gresswell and Varley 1988). Subsequent surveys in 1987 indicated that brook trout appeared to have been eradicated from the Arnica Creek drainage. Even more extensive has been the program implemented to protect the native golden trout in California from the negative effects of interactions with non-native salmonids (Pister, E. P., California Department of Fish and Game, personal communication; Pister 1991). Hundreds of kilometers of stream have been chemically treated to eradicate brown and rainbow trout in the South Fork of the Kern River drainage and brook and rainbow trout in the Little Kern River drainage. Major barriers to fish movement were also constructed to prevent re-invasion from downstream areas. Although eradication of non-native species has been successful in these cases, the costs for such programs have been substantial. Sometimes, eradication of a naturalized species may be technologically impossible when the species occurs over a wide geographic area (e.g., sea lamprey, *Petromyzon marinus*, in the Great Lakes; Smith and Tibbles 1980).

Conclusion

Introductions of non-native salmonids have had serious deleterious ecological and genetic effects on native salmonids at some locations in North America. Best studied have been the effects of the introduction of rainbow trout on native cutthroat and golden trout in the western part of the continent and on brook trout in the east. Competition, predation, and hybridization by the introduced species appear to be the primary processes which affect native salmonids. If the statistical power of field studies has been characteristically weak (see Peterman 1990), then the actual effects of salmonid introductions could be much worse than reported here.

Unequivocal evidence is lacking in most cases to support the conclusion that competition is an important mechanism that causes displacement of native species. Often studies of competition have to be simplified in design and time frame, and conducted under comparatively artificial conditions due to logistical practicality. Subsequently, results must be interpreted and extrapolated to natural conditions. The difficulties of this approach may be illustrated by the results reported by Cunjak and Green (1984, 1986) that suggested rainbow trout had little competitive advantge over brook trout in experimental channels, yet field observations suggest otherwise in Appalachian streams (Larson and Moore 1985) and Great Lakes tributaries. If possible, studies should be conducted through the direct manipulation of species densities in replicated stream sections (Fausch 1988) similar to those conducted on the effects on brook trout numbers when rainbow trout were removed from Appalachian streams (Moore et al. 1983, 1986). This approach should also be useful in elucidating the role of introduced salmonid predators (e.g., Shetter and Alexander 1970).

Clear documentation does exist for hybridization between native and introduced salmonids because of the availability of laboratory techniques such as allozymic analyses that unequivocally identify species and their hybrids. In contrast, data that provide indisputable evidence for the inter-breeding of stocks of the same species are generally lacking. Similar to studies of competition, examination of the potential for inter-breeding would best be conducted through replicated manipulative experiments conducted in natural environments with genetically distinct stocks rather than the correlative approaches used in the past (e.g., Krueger and Menzel 1979). Few data exist regarding the second generation contributions of intraspecific hatchery plantings which constitute by far the largest category of salmonid introductions. The potential negative impact on the resident gene pool argues that management agencies should try to measure the genetic effects of their stocking programs.

What about the future? Should introductions of new salmonid species or stocks continue? Below we offer five recommendations about future salmonid introductions. The recommendations were developed on the premise that the risks or costs associated with salmonid introductions should be borne by society and not by native species or populations.

First, some introductions are acceptable, especially those used in restoration programs for populations or those used in threatened or endangered species programs. Examples include the restoration of lake trout in the Great Lakes and of Atlantic salmon in rivers along the Atlantic coast. Considerations for stocking fish will be different depending on whether or not local extinction or severe population depletion has occurred (Krueger et al. 1981; Williams et al. 1988). If local extinction has not occurred, stocking strategies should seek to protect the original

native gene pool that remains. Unusual man-made or man-altered environments, such as reservoirs, may also provide acceptable locations for stocking programs. The fish species used for these introductions should have the characteristics suggested by Li and Moyle (1981).

Second, we recommend termination of the continued stocking of non-native trout and salmon species or strains if these fish will have direct access to or contact with wild native salmonid populations. This type of introduction poses unacceptable ecological and genetic risks. Implicit within this recommendation is the belief by the authors that native salmonid species and strains have a priority for existence and perpetuation over non-native forms. If societal pressures on fishery management requires implementation of put-grow-take, enhancement, or supplementation programs, then local native species and stocks should be used for propagation and stocking. If these stocking programs occur in bodies of water where other species are being restored, careful consideration must be given to determine whether the two programs conflict with each other. We argue that if a choice is to be made between the two types of programs, native species or population restoration should be given the highest priority. In some circumstances, following this recommendation may not be straight forward. For example, "What is a native species or stock?" Anadromous rainbow trout were introduced approximately 100 yr ago to Lake Superior and have developed self-sustaining populations that support a highly prized sport fishery. Many anglers in the region consider rainbow trout a native and the more recently introduced chinook salmon as an exotic. In this case, the distinction between native and exotic species by society appears dependent on the time since introduction, with the transition from exotic to native measured, at most, in a few human generations rather than glacial epoches.

Third, we suggest that no new introductions of European or Asian salmonid species should occur in North America because of the unpredictable ecological and genetic effects on native species. Further, new intracontinental transfers of salmonid species or stocks is also discouraged. Lakes and streams can be considered as islands of aquatic environments in a sea of land (Magnuson 1976; Brown 1989). Their community dynamics are likely to operate similarly to the processes and concepts used to explain island biogeography (MacArthur and Wilson 1967). This theory predicts that such islands are more susceptible to successful invasion by alien species with subsequent extinction of native species than larger, less isolated, and more complex environments. Waters suitable for salmonids may be even more prone to vulnerability from invasion than other lakes and streams because they are typically oligotrophic and have low species diversity. Li and Moyle (1981) suggest that these waters are simply not good sites for new introductions due to the potential negative effects on native fauna. Thus, ecological theory predicts that native salmonids and their aquatic communities appear to be at a higher risk of extinction through interactions with introduced fish than would occur in other aquatic communities. The amount of information needed to develop better quantitative predictions of the effects of introductions would be more than is available for any vertebrate species (Brown 1989). Simply stated, the risk posed by new introductions to native faunas is too high and unpredictable to justify further introductions.

Fourth, technology must be developoed and policies enacted that help minimize the risk from escapement of cultured salmonids into the wild. Salmon and trout that escape from the salmonid pen or cage culture industry pose important ecological and genetic risks to wild populations. Fortunately, lost fish pose important economic costs to the industry, thus a strong incentive exists to consider measures to prevent escapement.

Fifth, transgenic fish, those that have had foreign DNA inserted into their genomes, pose yet another threat to wild salmonid populations. Measures need to be in place to prevent the release or escapement of these fish into the wild (see discussions by Tiedje et al. 1989 and Kapuscinski and Hallerman 1990). For example, Atlantic salmon populations are already at risk from this type of introduction as the antifreeze protein gene has been reported to have been successfully transferred into the Atlantic salmon genome (Fletcher et al. 1988).

Certainly, not every introduction of non-native salmonids has caused a permanent ecological or genetic effect on native North American fauna. The lack of detectable effects on native salmonids from introductions has been reported (e.g., Miller 1958; Pollard and Bjornn 1973; Petrosky and Bjornn 1988) and has been argued to be the most common result of introductions in general (Simberloff 1981). Regardless, the chronic, long-term practice of stocking non-native salmonids over the past century has contributed major, and seemingly permanent, changes in the native salmonid species of the continent. The pervasive and permanent nature of such biological contamination of aquatic communties by exotic species and the difficulty of remediation makes the risk from non-native introductions too high.

For approximately 100 yr after 1870, the manipulation of aquatic communities by the introduction of non-native species was viewed as ethically acceptable by fisheries professionals in North America. Undeniably, the stocking of non-native salmonids resulted in the development of important sport fisheries throughout the continent. Since that time, fishery science has questioned the continued acceptability of such practices on the basis of ecological and genetic theory (e.g., Magnuson 1976; Li and Moyle 1981). The legitimacy of new introductions appears to have declined considerably among fishery professionals as policies and measures have been developed to control future introductions of fish (e.g., Welcomme 1986; Kohler and Courtenay 1986; Hallerman and Kapuscinski 1990). In a broader context, a new discipline has concurrently emerged since 1970, known as conservation biology, that explicitly places high value on natural assemblages of organisms and their protection, and discourages non-native introductions (e.g., Soulé 1986). Clearly, the era of widespread, intentional introductions of salmonids and other fish species as a fishery management activity justifiably is drawing to a close.

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Molecular Genetics: Stock Identification and Manipulation

Mitochondrial DNA Diversity in Fishes and its Implications for Introductions[1]

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Billington, N., and P. D. N. Hebert. 1991. Mitochondrial DNA diversity in fishes and its implications for introductions. Can. J. Fish. Aquat. Sci. 48 (Suppl. 1): 80–94.

Patterns of mitochondrial DNA (mtDNA) variation have now been examined in more than 40 fish species. This work has established that mitochondrial genomes of fish show constrained size variation, but that genomes of closely related species often vary in size, suggesting that counterbalancing deletions and insertions act to stabilize genome size. Gene order and composition are also stable, but nucleotide sequences show rapid divergence. Populations of most fish species contain a few common mtDNA haplotypes and a spectrum of their rare mutational derivatives. The extent of genetic divergence among dominant haplotypes seems linked to environmental conditions with greater divergence in freshwater than marine species, especially those occupying unglaciated localities. Haplotype frequencies ordinarily show considerable local divergence, largely as a result of stochastic shifts associated with population founding events. Such divergence provides a basis for both the discrimination of local stocks and for the recognition of major genetic discontinuities reflecting past episodes of gene pool fragmentation. Analysis of hatchery stocks has often revealed their mtDNA divergence, but in most cases stocks are fixed for haplotypes which are also common in wild populations. There is, however, the opportunity to develop broodstocks marked with rare haplotypes, permitting their recognition in nature over many generations.

On a étudié jusqu'à maintenant les variations de l'ADN mitochondrial (ADNmt) chez plus de 40 espèces de poissons. Les résultats indiquent que la taille du génome mitochondrial des poissons varie de façon limitée, mais que la taille du génome d'espèces apparentées varie souvent, ce qui laisse supposer que des mécanismes compensateurs de délétion et d'insertion entrent en jeu pour stabiliser la taille du génome. L'ordre et la composition des gènes sont également stables, mais une divergence dans les séquences de nucléotides apparaît tôt dans l'évolution de ces espèces. Les populations de la plupart des espèces de poissons possèdent quelques haplotypes d'ADNmt communs et une gamme d'haplotypes mutants rares. L'importance de la divergence génique entre les haplotypes dominants semble liée aux conditions environnementales, car la divergence est plus prononcée chez les espèces d'eaux douces que chez les espèces marines, et plus particulièrement chez les espèces vivant dans des régions épargnées par les glaciations. Généralement, la fréquence des haplotypes présente une divergence locale considérable en grande partie attribuable à des changements stochastiques qui sont liés aux conditions d'établissement des populations. Cette divergence fournit un point de départ pour distinguer les stocks locaux et pour reconnaître les hiatus génétiques importants qui reflètent des épisodes antérieurs de la fragmentation du pool génique. On a souvent observé une divergence au niveau de l'ADNmt dans des stocks d'élevage, mais dans la plupart des cas, les haplotypes qui sont également communs dans les populations sauvages ne varient pas. Toutefois, il est possible de créer des stocks reproducteurs marqués avec des haplotypes rares, ce qui permettrait leur détection en milieu naturel durant de nombreuses générations.

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Over the past decade it has been recognized that the optimal management of fish populations requires information on stock structure so that genetically divergent populations can be preserved. The earlier neglect of genetic diversity in fisheries management decisions was due to both the lack of tools for the determination of genetic variation and to an emphasis placed on the use of morphological characters for evaluating variation among populations. It was also a consequence of the lack of clear objectives in management programs concerning the maintenance of genetic diversity (Allendorf et al. 1987).

The introduction of allozyme analysis in the early 1970s provided an initial basis for the quantitative assessment of fish population structure and the application of this information to the problems of stock identification (Allendorf et al. 1987). Although allozyme markers have been employed in work on both natural populations (e.g. Clayton et al. 1974; Phillip et al. 1983; Ihssen et al. 1988) and hatchery stocks (Allendorf and Phelps 1980; Ryman and Stahl 1980), their value has been constrained because many species lack sufficient gene frequency divergence at polymorphic loci to permit population discrimination.

Techniques are now available which permit the identification of an unlimited number of genetic markers by examining variation at the DNA level. Hallerman and Beckmann (1988)

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review the advantages (in particular, enhanced resolution) and disadvantages (mainly cost and technical complexity) of DNA-level analyses in fishery management. Of these techniques, the examination of mitochondrial DNA (mtDNA) variation has been particularly widely adopted. Ferris and Berg (1987) examined the potential utility of mtDNA analysis for fish population genetics and fishery management, but at the time of their review there were few studies examining mtDNA diversity in fish. This lack of data has now been remedied. The current review describes the nature and extent of mtDNA diversity in fish, assesses the usefulness of such diversity in stock identification, and discusses the implications of this diversity for evaluating the impacts of fish introductions.

Features of Mitochondrial DNA

Animal mtDNA is a circular molecule usually ranging in size from 14 000 to 26 000 base pairs (bp). It is present in high copy number per cell making it relatively easy to purify (Brown 1983). Generally, mtDNA is homoplasmic, that is, all the molecules are identical in an organism, meaning that any tissue can be used as a source. The rate of nucleotide substitution in the mtDNA of higher vertebrates is approximately 5–10 times that of the nuclear genome, enhancing the resolution capacity for population-level studies (Brown 1983; Moritz et al. 1987). Mitochondrial DNA is maternally transmitted and is not subject to recombination (Hutchinson et al. 1974; Gyllensten et al. 1985b; Avise and Vrijenhoek 1987).

In philopatric fish species these characteristics have the effect of generating more genetic divergence in the mitochondrial than in the nuclear genome. The extent of genetic divergence among both segments of the genome is determined by the interaction of processes such as natural selection and genetic drift, which promote divergence, and gene exchange which reduces it. When populations are reasonably large and selection pressures weak, gene frequency divergence in the nuclear genome can be suppressed by modest flow arising from the movement of individuals of either sex. Thus, in the case where females are philopatric and males disperse during spawning, no divergence in the nuclear genome will occur. However, this same pattern of gene exchange permits divergence of the mitochondrial genome because of its maternal inheritance.

Maternally inherited mtDNA is also more likely to show differences among populations than nuclear DNA because its smaller effective population size (1/4 that of the bisexually inherited diploid nuclear genome if the sex ratio is 1:1) means that it is more susceptible to reductions in genetic variability due to population bottlenecks (Nei and Tajima 1981; Birky et al. 1983). Moreover, assuming equal migration ability of both sexes, four times as much interchange among populations is required to prevent divergence in the mitochondrial, as opposed to the nuclear genome in populations which are now genetically similar. Conversely, four times as much migration is required to erode existing divergence in mtDNA haplotype frequencies as to erode gene frequency differences at nuclear loci.

Gene Order

The mitochondrial genomes of animal taxa carry genes coding for 13 proteins, 22 tRNAs and 2 rRNA molecules, in addition to a noncoding region which contains the origin of heavy strand replication (D-loop region in vertebrates). It is now clear that gene order in the mitochondrial genome is highly conserved (Moritz et al. 1987). Sequencing studies have shown that gene order is identical in five different vertebrate taxa which span the range from amphibians (Roe et al. 1985) to mammals (Anderson et al. 1981, 1982; Bibb et al. 1981; Gadaleta et al. 1989). Joint mapping/hybridization studies have confirmed that a similar gene order exists in fish (*Cyprinus* — Araya et al. 1984; *Salmo* — Davidson et al. 1989; *Oncorhynchus* — Thomas and Beckenbach 1989; *Gadus* — Johansen et al. 1990). Although no fish mitochondrial genome has yet been completely sequenced, sections of the genome have been sequenced in white sturgeon, *Acipenser transmontanus* (Gilbert et al. 1988; Brown et al. 1989; Buroker et al. 1990), salmonids of the genera *Salmo* (Davidson et al. 1989) and *Oncorhynchus* (Davidson et al. 1988; Thomas and Beckenbach 1989), and Atlantic cod, *Gadus morhua* (Johansen et al. 1990).

Genome Size, Length Variation and Heteroplasmy

In comparison to those of fungi, plants, and protists (Wallace 1982), animal mitochondrial genomes show little variation in size, usually ranging from 14–26 kilobase pairs (kbp) in length. Some exceptions have been noted, for instance, a 39 kbp mtDNA molecule in the scallop, *Placopecten magellanicus* (Snyder et al. 1987). Among vertebrates, mammalian mtDNAs appear to be relatively uniform in size, whereas those of lower vertebrates show more length variation (Brown 1983; Bermingham et al. 1986; Moritz et al. 1987). Such length variation has an erratic phylogenetic distribution, with mtDNA from some groups such as amphibians spanning the entire size range (Moritz et al. 1987).

Mitochondrial genomes of fish vary little in size, with a range of 15.2–19.8 kbp reported among the 47 species analysed to date (Table 1). Some of the smaller size values are likely underestimates, as they were obtained in studies that employed techniques which did not permit the detection of restriction fragments under 0.5 kbp. Based on this size stability, one might expect that length variation in mitochondrial genomes among closely related fish species would be rare, but this is not the case. Variation in mtDNA size has been recorded between two genera in the family Scorpaenidae (Beckwitt and Petruska 1985) and between two genera (*Hucho, Salvelinus*) of salmonines (Grewe et al. 1990). In other cases (Table 2), size divergence has been noted among both conspecific individuals and among the mitochondrial from a single individual (i.e. length heteroplasmy). In all cases where such inserts have been mapped, they were located in the D-loop region. Length variation in mtDNAs of other animal species has also been mapped to the same region, suggesting that it is less impacted by the effects of insertions than are those areas of the molecule that code for functional genes (Brown 1983; Moritz et al. 1987).

Possible mechanisms for the production of length variation include replication slippage, duplication and deletion (Moritz et al. 1987). Buroker et al. (1990) suggested that length heterogeneity in white sturgeon (*Acipenser transmontanus*) was the result of frequent competitive misalignment in an 82 bp repeat region prior to replication. However, most inserts in fish mtDNA appear to be due to tandem duplications. A series of 100 bp length increments were noted in *Morone saxatilis* mtDNA (Chapman 1987; Wirgin et al. 1989) and 3–10 copies of a 110 bp repeat were observed in *Morone americana* (Mulligan and Chapman 1989). Bentzen et al. (1988) observed two mtDNA size classes (18.3 kbp and 19.8 kbp) in American shad (*Alosa sapidissima*), due to a 1.5 kbp tandem repeat, which

TABLE 1. Reported lengths of mitochondrial DNA molecules in fish species (reported as range, or ± 1 SE as given in the reference).

Family species	Size (bp)	Reference
Amiidae		
Amia calva	16 000 – 16 900	Bermingham et al. (1986)
Clupeidae		
Alosa sapidissima	18 300 – 19 800	Bentzen et al. (1988)
Clupea harengus harengus	16 990 ± 620	Kornfield and Bogdanowicz (1987)
Clupea harengus pallasi	16 730 ± 260	Schweigert and Withler (1990)
Galaxiidae		
Galaxias truttaceus	16 230 ± 220	Ovenden and White (1990)
Salmonidae		
Coregonus artedii	16 945 ± 240	Bernatchez and Dodson (1990)
Hucho hucho	17 500 ± 200	Grewe et al. (1990)
Oncorhynchus tshawytscha	16 670	Berg and Ferris (1984)
Oncorhynchus tshawytscha	16 500 ± 440	Wilson et al. (1987)
Oncorhynchus tshawytscha	16 500 ± 500	Thomas et al. (1986)
Oncorhynchus gorbuscha	16 500 ± 500	
Oncorhynchus keta	16 500 ± 500	
Oncorhynchus kisutch	16 500 ± 500	
Oncorhynchus nerka	16 500 ± 500	
Oncorhynchus mykiss	16 500 ± 500	
Oncorhynchus mykiss	15 560	Palva and Palva (1987)
Salmo gairdneri	16 670	Berg and Ferris (1984)
Salmo trutta	16 670	
Salmo salar	16 700	Birt et al. (1986)
Salmo salar	16 480 ± 480	Hovey et al. (1989)
Salmo salar	16 640 ± 450	Palva et al. (1989)
Salvelinus alpinus	16 800 ± 200	Grewe et al. (1990)
Salvelinus confluentus	16 800 ± 200	
Salvelinus malma	16 800 ± 200	
Salvelinus namycush	16 800 ± 200	
Salvelinus fontinalis	16 800 ± 200	
Salvelinus fontinalis	16 670	Berg and Ferris (1984)
Cyprinidae		
Carassius auratus	16 100 ± 220	Beckwitt and Aoyagi (1987)
Carassius auratus	15 210	Guanjun et al. (1984)
Cyprinus carpio	16 990	
Cyprinus carpio	16 400	Araya et al. (1984)
Tribolodon hakonensis	16 400 ± 600	Hanzawa et al. (1987)
Zacco temmincki	16 700	Lee et al. (1988)
Ariidae		
Arius felix	16 600	Avise et al. (1987b)
Bagre marinus	16 600	
Batrachoidae		
Opsanus tau	19 500	
Opsanus beta	19 500	
Gadidae		
Gadus morhua	16 000	Smith et al. (1989)
Gadus morhua	16 500	Johansen et al. (1990)
Cyprinodontidae		
Fundulus heteroclitus	17 200 ± 300	González-Villaseñor et al. (1986)
Gasterosteidae		
Gasterosteus aculeatus	16 600	Gach and Reimchen (1989)
Trachichthyidae		
Haplostethus atlanticus	16 210 ± 820	Ovenden et al. (1989)
Centropomidae		
Centropomus undecimalis	17 400	Mangini et al. (1985)
Percichthyidae		
Morone americana	17 500 – 19 000	Mulligan and Chapman (1989)
Morone saxatilis	17 500 – 17 900	Chapman (1987)
Morone saxatilis	17 500 – 17 900	Wirgin et al. (1989)
Centrarchidae		
Lepomis macrochirus	16 200	Avise et al. (1984)
Percidae		
Stizostedion vitreum	16 860 ± 160	Billington and Hebert (1988)
Stizostedion canadense	16 790 ± 130	Billington et al. (1988)
Stizostedion lucioperca	16 790 ± 60	Billington et al. (1990)

TABLE 1. (*Concluded*)

Family species	Size (bp)	Reference
Gadopsidae		
Gadiopsis marmoratus	16 300 ± 200	Ovenden and White (1988)
Scombridae		
Katsuwonus pelamis	16 900	Graves et al. (1984)
Thunnus alalunga	16 750 ± 200	Graves and Dizon (1989)
Scomber japonicus	17 200 ± 400	Beckwitt and Petruska (1985)
Scorpaenidae		
Scorpaena guttata	19 500 ± 300	Beckwitt and Petruska (1985)
Sebastes atrovirens	17 300 ± 400	
Sebastes caurinus	17 400 ± 400	
Sebastes melanostomus	17 200 ± 400	
Sebastes mystinus	16 900 ± 400	

TABLE 2. Length variation (I — insertion; D — deletion) and heteroplasmy (LH — length heteroplasmy; SH — site heteroplasmy) in fish mtDNA, with frequency of occurrence in each survey. All lengths are in base pairs.

Species	Frequency (%)	Variant size	Type	Reference
Acipenser transmontanus	41	82*	LH	Buroker et al. (1990)
Alosa sapidissima	12	1500	LH	Bentzen et al. (1988)
	4	—	SH	
Amia calva	8	450–900	I LH	Bermingham et al. (1986)
Merluccius capensis	12	200	D	Becker et al. (1988)
	25	400	I	
Morone americana	100	110+	I LH	Mulligan and Chapman (1989)
Morone saxatilis B	45	100	I	Chapman (1987, 1989)
C	38	200	I	
D/E	3	150/250	I LH	
F	6	300	I	
Morone saxatilis B	7	200	I	Wirgin et al. (1989)
C	58	300	I	
D	28	400	I	
	20		LH	
Salvelinus namaycush	1	20	LH	Grewe and Hebert (1988)
Stizostedion vitreum	2	1700	I	Billington and Hebert (1988)
	2	130	I	Ward et al. (1989)

N.B. Letters identifying size classes for *Morone saxatilis* are different in each of the two above studies.

* — 3–5 copy repeat.

+ — Multiple copies, 3–10 per individual.

was present in two copies in the smaller and three copies in the larger size class. Interesting, fish with the larger size class of mtDNA were invariably heteroplasmic. Smaller 40 bp length variants were also detected within the 1500 bp repeats. Bentzen et al. (1988) also found an heteroplasmic *Sal* I restriction site in 4% of shad, and suggested that both site and length heteroplasmy had arisen independently in different mtDNA lineages. Two different mtDNA size variants (1700 bp, 130 bp) which apparently represent tandem duplications have been detected in a small percentage of walleye, *Stizostedion vitreum* (Billington and Hebert 1988; Ward et al. 1989). Length variants among mtDNA genotypes of the southern African hake, *Merluccius capensis*, were attributed to a 200 bp deletion and a 400 bp addition in the lineages leading to the most common genotype (Becker et al. 1988).

Chapman (1987, 1989) and Wirgin et al. (1989) noted that length variation was more common than restriction site variation in striped bass and that the incidence of length variants differed among stocks. However, the usefulness of length variants for stock discrimination remains uncertain until their transmission genetics are more completely understood. For example, it is uncertain if heteroplasmic individuals transmit variants to their offspring (Mulligan and Chapman 1989).

Molecular Clock Calibration

Brown et al. (1979) showed that the rate of mtDNA sequence divergence for several mammalian species (mainly primates) was approximately 2% per million years and remained linear for 8–10 million years. Additional studies have generally

confirmed this rate for other homeotherms (Brown 1983), including birds (Shields and Wilson 1987). This molecular clock calibration has been employed to estimate the divergence times among salmonids (Wilson et al. 1985; Thomas et al. 1986; Bernatchez et al. 1988, 1989; Grewe et al. 1990) centrarchids (Bermingham and Avise 1986) and percids (Billington and Hebert 1988; Billington et al. 1990).

Although Billington et al. (1990) found good agreement in divergence times among *Stizostedion* species estimated from both allozyme and mtDNA data, it is clear that caution should be employed in assuming the rate constancy of mtDNA evolution. For example, Bentzen (1988) concluded that the rate of mtDNA evolution in the fish genus *Alosa* was only 1/10 of that found in higher vertebrates. Dowling and Brown (1989) suggested that mtDNA divergence rate heterogeneity might be responsible for incongruencies between allozyme and mtDNA phylogenies for four *Notropis* species. Moreover, there are inconsistencies in the divergence times of some salmonids estimated from mtDNA and fossil data (Grewe et al. 1990), suggesting that the rate of mtDNA evolution in salmonids is approximately 1/3 to 1/2 of that of higher vertebrates (G. R. Smith, Museum of Zoology, University of Michigan, Ann Arbor, Michigan, pers. comm.). Thomas and Beckenbach (1989) noted that divergence estimates among six *Oncorhynchus* species obtained from restriction site data were lower than those obtained from sequence analysis. They suggested that this was due to an increased probability of multiple changes within a restriction site, especially as the level of sequence divergence increased. Divergence values corrected for multiple hits (Thomas and Beckenbach 1989) fit well with the 1/3 to 1/2 decreases in rate noted above. Ultimately, resolution of this apparent rate heterogeneity will be decided by more detailed analysis of fish taxa which have diverged in the last 10 million years, and for which there are comprehensive fossil records.

Methods of mtDNA Analysis in Fish

Mitochondrial DNA is usually obtained from fresh liver or gonadal tissues because of their high mitochondrial densities, but essentially any other tissue may be used (Chapman and Brown 1990). Normally, nuclei are removed from the tissue homogenate by low speed centrifugation, and mitochondria are then pelleted and mtDNA released by membrane lysis. In rapid preparation methods (e.g. González-Villaseñor et al. 1986; Bernatchez et al. 1988), protein contaminants are removed by organic extraction with phenol and chloroform, and the DNA collected by ethanol precipitation. Alternatively, mtDNA may be purified using cesium chloride density gradient centrifugation (Ferris and Berg 1987; Billington and Hebert 1988). Chapman and Brown (1990) review the various methods for isolating mtDNA and discuss the criteria for choosing a particular isolation method.

The study of mtDNA variation to date is largely based upon digestion of the molecule using restriction endonucleases and separation of the resulting fragments according to molecular weight by gel electrophoresis. Fragments may be visualized either by ethidium bromide staining, or by autoradiography following end-labelling with radionucleotides. Variability in fragment patterns is interpreted as genetic variation at the nucleotide level. Thus, a nucleotide substitution in the molecule that causes the loss or gain of a nucleotide sequence recognized by a specific restriction enzyme will cause a change in the observed fragment pattern.

An alternative method is the visualization of mtDNA bands in total DNA digests via use of a radiolabelled mtDNA probe (Mangini et al. 1985; González-Villaseñor et al. 1986; Ferris and Berg 1987). Modifications of this technique allow the determination of mtDNA markers without the need to sacrifice fish (Billington and Hebert 1990). Detailed accounts of mtDNA extraction and analytical protocols are provided elsewhere (e.g. González-Villaseñor et al. 1986; Ferris and Berg 1987; Billington and Hebert 1988, 1990; Chapman and Brown 1990).

A recent innovation has been the use of the polymerase chain reaction (PCR) to amplify DNA obtained from extremely small amounts of tissue. This technique allows short segments (<500–2000 bp) of DNA to be directly sequenced, eliminating the need for vector cloning and providing a very fine level of resolution. As DNA can be isolated from preserved or even fossilized material, it provides an opportunity for comparison of DNA sequence divergence in extinct species, or in museum specimens of very rare taxa (Arnheim et al. 1990; Thomas et al. 1990). The use of this technique to study fish mtDNA is described by Beckenbach (1991). Recent studies demonstrate the utility of this technique for examining interspecific (*Thunnus* species — Bartlett and Davidson 1991) and intraspecific (*Gadus morhua* — Carr and Marshall 1991) relationships in fish.

Mitochondrial DNA Diversity at the Supraspecific Level

Sequence divergence estimates can be derived from a comparison of congruence in fragment patterns, or from direct comparison of shared restriction sites or nucleotide sequences (e.g. Nei et al. 1985). The former method suffers from the disadvantage that taxa which share restriction sites may share no fragments. Moreover, site characters are preferred to fragment characters as fragment data provide redundant information concerning a single evolutionary event (the gain or loss of a restriction site) (Bermingham 1990). When the haplotypes are closely related site gains and losses can be inferred from fragment data. Analysis of shared restriction sites requires detailed mapping studies, which are time consuming. Direct sequence analysis of PCR amplified segments of the mitochondrial genome avoids the difficulties inherent in map alignment and offer the best possibility of rapid assessment of sequence divergence.

Reported sequence divergence values for congeneric fish range from 3.7–13% for marine, estuarine and catadromous species, and from 0.4–100% for freshwater and anadromous species (Table 3). The very high values (up to 100% — Table 3) obtained among *Lepomis* species by Avise and Saunders (1984) are obviously overestimates arising from the fragment comparison methods used. Although there were no fragments in common, there was undoubtedly sequence similarity at many sites in the mtDNA molecules of these species. Other comparisons may be underestimates. For example, the low sequence divergence values observed among putative "species" in the Arctic char complex may be a consequence of flawed taxonomy (Grewe et al. 1990). When these exceptions are excluded, mtDNA divergence among congeneric fish ranges from 1.4–16% (Table 3), values similar to those reported for other vertebrates (Tegelström et al. 1988).

Systematic Relationships

Due to its rapid rate of evolution, mtDNA analysis has proven useful in clarifying relationships among closely related species.

TABLE 3. Sequence divergence (%) of mtDNA among congeneric fish taxa.

Species	%	Reference
Freshwater and Anadromous		
Oncorhynchus spp.	2.0–3.5	Wilson et al. (1985)
	1.7–6.7	Ginatulina et al. (1989)
	2.5–6.9	Thomas et al. (1986)
Salvelinus spp.	3.1–3.6	Grewe and Hebert (1988)
	0.4–4.3	Grewe et al. (1990)
Coregonus spp.	1.4–5.9	Bernatchez et al. (1990)
Poeciliopsis spp.	11.5	Avise and Vrijenhoek (1987)
Stizostedion spp.	8.1–15.7	Billington et al. (1990)
Notropis spp.	14.0	Dowling and Brown (1989)
Lepomis spp.	7.0–100	Avise and Saunders (1984)
Gadopsis spp.	6.6	Ovenden et al. (1988)
Marine, Estuarine and Catadromous		
Anguilla spp.	3.7	Avise et al. (1986)
Opsanus spp.	10.1	Avise et al. (1987b)
Merluccius spp.	11.6	Becker et al. (1988)

For example, Avise et al. (1986) confirmed the taxonomic validity of two eel species (*Anguilla anguilla* and *A. rostrata*) by establishing that fixed differences in their mitochondrial DNA were detectable with 11 of 14 restriction enzymes. Previously, their distinctiveness had been questioned because morphological differences between the two taxa were linked to environmental effects, and only a single diagnostic locus was found using allozyme analysis. Berg and Ferris (1984) employed mtDNA analyses to show that *Salmo gairdneri* was much more closely related to *Oncorhynchus tshawytscha* than it was to either *Salmo trutta*, or *Salvelinus fontinalis*. Additional studies (Thomas et al. 1986; Gyllensten and Wilson 1987) have confirmed that *S. gairdneri* and *Salmo clarki* were more closely related to members of the genus *Oncorhynchus* than to *Salmo*, providing further evidence to support the transfer of these taxa to *Oncorhynchus* (Smith and Stearley 1989). Other systematic studies have examined both the relationships within single salmonid genera including *Salvelinus* (Grewe et al. 1990) and *Coregonus* (Bernatchez et al. 1988), as well as among genera (Bernatchez et al. 1988; Ginatulina et al. 1989; Grewe et al. 1990). Recently, Bartlett and Davidson (1991) used direct sequence analysis of the mitochondrial cytochrome *b* genes, following PCR amplification, to identify four different species of tuna (*Thunnus*).

Billington et al. (1990) examined relationships among three members of the percid genus *Stizostedion* using both allozyme and mtDNA analyses, and found that both methods showed that the two North American species (*S. vitreum* and *S. canadense*) were more closely related to each other than either was to the European species, *S. lucioperca*. The results of mtDNA analyses in other systematic studies have been more equivocal. Dowling and Brown (1989) found that mtDNA data failed to provide greater taxonomic resolution among four *Notropis* species than allozyme analyses, possibly due to rate heterogeneity and introgression. Similarly, phylogenetic relationships among taxa in the Arctic char complex derived from mtDNA data, while consistent with chromosomal studies, differed from those based on morphological analyses (Grewe et al. 1990). Furthermore, different branching orders were obtained in two mtDNA studies of the systematic relationships among *Oncorhynchus* species (Thomas et al. 1986; Ginatulina et al. 1989).

Hybridization, Introgression and Unisexual Species

As a group, fish show high levels of interspecific hybridization primarily associated with their employment of external fertilization (Mayr 1963). Hybridization is considerably more common among freshwater than marine fishes, perhaps because most freshwater habitats are of relatively recent origin compared to oceans (Mayr 1963; Campton 1987). Thus, many freshwater species in the Northern Hemisphere evolved during the Pleistocene and isolating mechanisms may not have been perfected. In other cases, hybridization may have been enhanced by secondary contact of fish species with partly developed isolating mechanisms as a result of introductions, the invasion of exotics, or interdrainage contacts due to diversion programs.

While study of genetic variation in the nuclear genome (e.g. allozyme analyses) is essential to ascertain the incidence of hybrids, mtDNA analysis can provide supplemental information on both the directionality of hybridization, and the incidence of introgression (Avise and Saunders 1984; Avise et al. 1984; Campton 1987; Billington et al. 1988). There are a growing number of examples of mtDNA exchange between closely related fish species (Table 4). In some cases, such as *Lepomis*, interspecific hybridization was infrequent and involved females of species that were rare (Avise and Saunders 1984). The resulting F_1 hybrids were mainly sterile and hence, introgression was not detected. In other cases, bi-directional transmission and/or introgression of mtDNA has been noted (Avise et al. 1984; Gyllensten et al. 1985a; Bentzen 1988; Billington et al. 1988; Bernatchez et al. 1989; Dowling and Brown 1989; Dowling et al. 1989).

In the minnows *Notropis cornutus* and *N. chrysocephalus*, allozyme data revealed frequency dependent introgression, with the rarer species at a locality exhibiting a higher proportion of introgressed alleles (Dowling et al. 1989). However, introgression of mtDNA haplotypes varied geographically, so that in westward flowing Michigan drainages, *N. cornutus* haplotypes were more common in F_1 hybrids and backcrosses independent of their parental frequencies. By contrast, in eastward flowing drainages, *N. chrysocephalus* mtDNA was more common. Dowling et al. (1989) suggested that this was due to either geo-

TABLE 4. Evidence of mtDNA exchange between fishes in natural systems. (I) – indicates introgression.

Species		Reference
UNIDIRECTIONAL		
Donor	Recipient	
Lepomis cyanellus	*L. macrochirus*	Avise and Saunders (1984)
Lepomis gulosus	*L. macrochirus*	
Lepomis microlophus	*L. macrochirus*	
Lepomis macrochirus	*L. microlophus*	
Lepomis auritus	*L. cyanellus*	
L. macrochirus purpurescens	*L. m. macrochirus* (I)	Avise et al. (1984)
Stizostedion canadense	*S. vitreum* (I)	Billington et al. (1988)
Stizostedion vitreum	*S. canadense*	N. Billington (unpubl. data)
Coregonus albula	*C. lavaretus* (I)	Bernatchez et al. (1989)
BIDIRECTIONAL		
Oncorhynchus clarki lewisi and *O. c. clarki* (I)		Gyllensten et al. (1985a)
Alosa fallax and *A. alosa*		Bentzen (1988)
Notropis chrysocephalus and *N. cornutus* (I)		Dowling et al. (1989)
Notropis cornutus, N. chrysocephalus, N. rubellus and *N. photogenis* (I)		Dowling and Brown (1989)

graphically variable patterns of selection against different hybrid and backcross combinations, or that genetic differences between fish in the two drainage systems accumulated during historical isolation. In another case, the introgression of sauger (*Stizostedion canadense*) mtDNA into the walleye (*S. vitreum*) genome appeared to be caused by the inadvertent stocking of a few female sauger, or sauger × walleye hybrids, into a walleye population (Billington et al. 1988). In general, hybridization events have the potential to complicate assessment of systematic relationships if introgressed mtDNA genomes rise to high frequencies in the recipient taxon, but are lost from the donor taxon. It is important to note, however, that highly divergent lineages found within a taxon may be the result of retained ancestral polymorphisms, rather than introgression (e.g. Avise et al. 1990).

Mitochondrial DNA analysis has also been used to determine the maternal parentage of unisexual fishes, whose origin has been linked to interspecific hybridization. For example, Avise and Vrijenhoek (1987) showed that *Poeciliopsis monacha* was the maternal parent of the unisexual hybrid taxon *P. monacha-lucida*. Similarly, Echelle et al. (1989) demonstrated that *Menidia peninsulae* was the female parent of the unisexual *M. clarkhubbsi*. Goddard et al. (1989) showed that *Phoxinus neogaeus* was the female parent of *P. eos-neogaeus* gynogens and concluded that multiple hybridization events had occurred, because the mtDNA haplotype of the unisexuals was identical to that of resident *P. neogaeus* at some sites, but different at others.

Mitochondrial DNA Diversity at the Species Level

Prior studies have made it clear that in most, if not all fish species, there are a few common haplotypes and a substantially larger number of rare haplotypes which are their mutational derivatives (Fig. 1). Comparisons of mtDNA diversity among species are complicated by the fact that the number of haplotypes detected is a function of both the number of fish examined and of the intensity of sampling of the genome (i.e. the number of fragments surveyed, which itself is a function of the number and type of endonucleases used). Thus, there is ordinarily a positive association between haplotype diversity and the number of fish examined, and the number of endonucleases employed in their analysis. The effect of sample size on the number of haplotypes detected can be removed through the use of diversity indices (e.g. Nei and Tajima 1981), but standardization of sampling effort on the genome is more difficult to achieve.

Aside from the desirability of comparing levels of diversity among different taxa, it is important to ascertain when sufficient effort has been expended on a single species to recognize essentially all of the mtDNA diversity present. This problem is analogous to the measurement of clonal richness in asexual organisms, where a combinatorial analytical technique (Hebert et al. 1988) has been employed. This same procedure has been used to examine mtDNA diversity. In whitefish, *Coregonus clupeaformis* and *C. laveratus*, Bernatchez et al. (1989) found a linear relationship between the number of endonucleases utilized and the number of haplotypes observed indicating that many more undetected mtDNA variants may exist. Similarly, they examined the relationship between the number of haplotypes detected and the number of fish surveyed at both populational and regional levels. They found that the number of haplotypes detected approached an asymptotic value of three with a sample size of 18 fish in single populations of *C. clupeaformis*, but found, on a regional level, that a sample size of 110 fish was insufficient to detect all of the mtDNA variation. By comparison, in *C. laveratus*, the number of haplotypes detected increased sharply with sample size, so that sample sizes of 21 individuals from single populations and 78 individuals from the Boothian Gulf were inadequate to detect all of the mtDNA variants present.

Avise et al. (1989) suggest that some vertebrates harbour sufficient polymorphism in their mtDNA sequence to permit individual fingerprinting by conventional restriction enzyme analysis. They noted that menhaden (*Brevoortia* sp.) exhibited so much mtDNA size and restriction site polymorphism to permit the unambiguous discrimination of a high proportion (32/33) of the conspecific individuals assayed. Such extreme

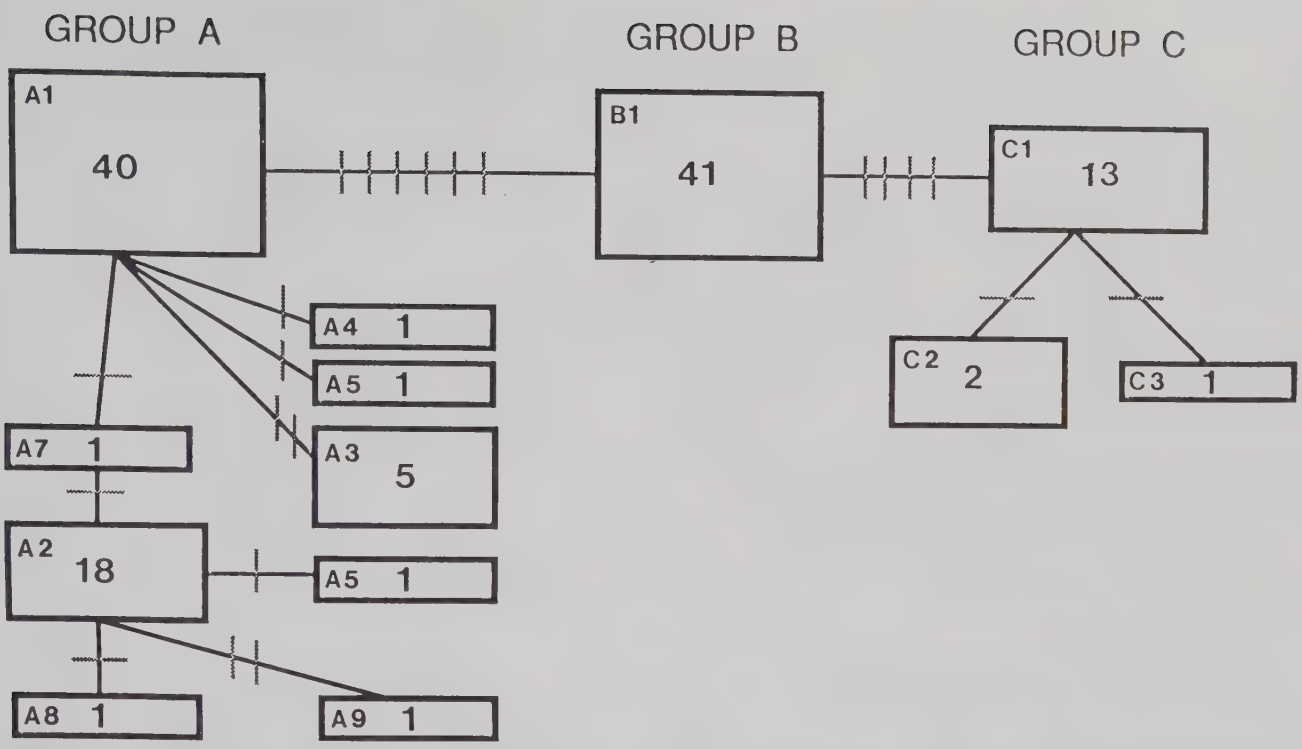

FIG. 1. Parsimony network of 13 lake trout (*Salvelinus namaycush*) mtDNA halotypes (boxes), modified from Grewe and Hebert (1988). Haplotype number and numbers of individuals possessing each haplotype are shown within the boxes. The number of restriction site changes differentiating each haplotype is indicated by dotted lines crossing the branches. The network shows the pattern of a few common distinct haplotypes (e.g. A1, B1, C1) and a larger number of less frequent haplotypes which are their mutational derivatives.

mtDNA variation also occurs in other fish species. For example, using a combination of 4, 5 and 6-base restriction endonucleases, Billington and Hebert (1986) were able to discriminate 32 of 33 walleye. Such mtDNA "fingerprints" could prove important in maternity analyses (Avise et al. 1989) by making it possible to discriminate among the progeny of individual female fish and thus to compare the relative contributions of individual females to juvenile recruitment.

Genetic Divergence among Haplotypes

Once mtDNA halotype diversity has been assessed, it becomes important to examine the extent of genetic divergence among haplotypes. High genetic similarity among haplotypes suggests that they were recently derived from a common ancestral haplotype, while greater divergence suggests a longer interval since their origin.

Divergence values as large as 10% have been reported among mtDNA haplotypes from single species of fish (Table 5). There is a report of 19.5% sequence divergence in *Zacco temminicki*, but this taxon is likely a complex of at least two species (Lee et al. 1988). Similarly, the high divergence values reported in menhaden (Avise et al. 1989) are not included as they may represent a species complex. Peak levels of divergence in freshwater species (10.0%) are greater than those in anadromous (5.0%), catadromous (2.0%), brackish (2.0%), or marine (4.4%) fish (Table 5). Ovenden (1990) also documented generally low mtDNA divergence values in marine organisms in a recent review, and suggested a number of possible explanations. These included a possible slower rate of mtDNA evolution in marine organisms, a lower diversity due to bottleneck effects, and family-specific mortality in species in which the offspring of individual females are grouped into egg-masses or schools. Clearly more work is needed to understand the origins of this difference in extent of mtDNA divergence between marine and freshwater taxa.

The extent of mtDNA variation in freshwater fishes in North America also appears related to geological events, with the least amount of sequence divergence observed in northern species and the greatest divergence occurring in species from unglaciated regions (Table 6). For example, Bermingham and Avise (1986) found clear geographical separation of the major mtDNA haplotypes of *Lepomis* species in the southern U.S. and sequence divergence values among these haplotypes are the highest yet identified in freshwater species. Conversely, some of the lowest values of sequence divergence occur among species whose current ranges were largely glaciated during the Pleistocene (Table 6). The reduced variation in these species is most probably due to the effects of reduced population size in glacial refugia causing bottlenecks. In species such as *S. namaycush* (Grewe and Hebert 1988), *S. vitreum* (Ward et al. 1989) and *C. artedii* (Bernatchez and Dodson 1990a), there is evidence of persistence in several refuges during the Wisconsin, but not in prior glaciations. By contrast, species from more southerly localities show the retention of mtDNA haplotypes which diverged at least one million years ago (Bermingham and Avise 1986).

Geographic Patterning in mtDNA Diversity

Programs to ensure the conservation of genetically divergent stocks of a fish species require, as a first step, the identification of such stocks. It is now evident that mtDNA diversity is an exceptionally useful tool in stock discrimination because it

TABLE 5. Intraspecific sequence divergence (%) of fish mtDNA.

Species	%	Reference
Freshwater		
Lepomis macrochirus	8.5	Avise et al. (1984)
Lepomis punctatus	0.2–4.2	Bermingham and Avise (1986)
Lepomis microlophus	0.2–10.0	
Lepomis gulosus	0.1–7.7	
Amia calva	0.2–1.2	
Carassius auratus	0.8	Beckwitt and Aoyagi (1987)
Tribolodon hakonensis	0.1–0.9	Hanzawa et al. (1987)
Gadopsis marmoratus	6.0	Ovenden et al. (1988)
Gadopsis bispinosus	8.9	
Stizostedion vitreum	0.2–0.6	Billington and Hebert (1988)
Salvelinus namaycush	0.2–1.2	Grewe and Hebert (1988)
Gasterosteus aculeatus	<1.0	Gach and Reimchen (1989)
Brackish		
Fundulus heteroclitus	2.0	González-Villaseñor and Powers (1990)
Menidia clarkhubbsi	0.2	Echelle et al. (1989)
Morone americana	0.1–5.0	Mulligan and Chapman (1989)
Anadromous		
Salmo salar	0.2–1.8	Palva et al. (1989)
Salmo salar	0.1–0.7	Bermingham (1990)
Oncorhynchus clarki	2.0	Gyllensten et al. (1985a)
Oncorhynchus mykiss	<1.0–1.5	Wilson et al. (1985)
Oncorhynchus mykiss	0.5	Thomas et al. (1986)
Oncorhynchus keta	0.2	
Oncorhynchus nerka	<0.2	
Oncorhynchus kisutch	<0.2	
Oncorhynchus tshawytscha	0.1–0.8	Wilson et al. (1987)
Coregonus lavaretus	0.3	Bernatchez et al. (1989)
Coregonus clupeaformis	0.2	
Coregonus clupeaformis	0.1–0.4	Bernatchez and Dodson (1990b)
Coregonus artedii	0.1–1.0	Bernatchez and Dodson (1990a)
Morone saxatilis	<0.1	Wirgin et al. (1989)
Alosa sapidissima	0.2	Bentzen et al. (1989)
Galaxias truttaceus	0.9	Ovenden and White (1990)
Catadromous		
Anguilla anguilla	<2.0	Avise et al. (1986)
Anguilla rostrata	<0.6	
Marine		
Merluccius capensis	2.2	Becker et al. (1988)
Merluccius paradoxus	0.9	
Arius felis	0.8	Avise et al. (1987b)
Bagre marinus	0.6	
Opsanus tau	0.9	
Opsanus beta	0.6	
Clupea harangus harangus	0.2–4.4	Kornfield and Bogdanowicz (1987)
Clupea harangus pallasi	0.2–1.8	Schweigert and Withler (1990)
Katsuwonus pelamis	<0.6	Graves et al. (1984)
Haplostethus atlanticus	0.2	Ovenden et al. (1989)

retains a history of past isolation in a way that the nuclear genome cannot. For example, if a single population becomes subdivided into two isolates, gene frequencies will diverge in both the nuclear and mitochondrial genomes as a result of drift and mutation (Fig. 2). In fact, populations may become rapidly fixed for different mtDNA types due to the effects of stochastic lineage extinction (Avise et al. 1987a). If these populations come into secondary contact, gene frequencies at variable loci in the nuclear genome initially show a step cline that gradually erodes until there is no evidence of past isolation. The erosion of mtDNA divergence follows a similar pattern, but occurs more slowly, and at the end of the process the populations contain two distinct mitochondrial lineages.

Ward et al. (1989) found evidence of this phenomenon in their comparison of mtDNA and allozyme variation in walleye (*Stizostedion vitreum*) across Canada. Walleye mtDNA hap-

TABLE 6. Maximum sequence divergence (%) of mtDNA among freshwater and anadromous fishes whose ranges were differentially affected by Pleistocene glaciation.

Species	%	Reference
UNGLACIATED		
Lepomis macrochirus	8.5	Avise et al. (1984)
Lepomis punctatus	4.2	Bermingham and Avise (1986)
Lepomis microlophus	10.0	
Lepomis gulosus	7.7	
Amia calva	1.2	
Gadopsis marmoratus	6.0	Ovenden et al. (1988)
Gadopsis bispinosus	8.9	
PARTIALLY GLACIATED		
Fundulus heteroclitus	2.0	González-Villaseñor and Powers (1990)
Morone americana	5.0	Mulligan and Chapman (1989)
Morone saxatilis	<0.1	Wirgin et al. (1989)
Alosa sapidissima	0.2	Bentzen et al. (1989)
Coregonus lavaretus	0.3	Bernatchez et al. (1989)
GLACIATED		
Stizostedion vitreum	0.6	Billington and Hebert (1988)
Salvelinus namaycush	1.2	Grewe and Hebert (1988)
Gasterosteus aculeatus	<1.0	Gach and Reimchen (1989)
Salmo salar	1.8	Palva et al. (1989)
Oncorhynchus clarki	2.0	Gyllensten et al. (1985a)
Oncorhynchus mykiss	1.5	Wilson et al. (1985)
Oncorhynchus keta	0.2	Thomas et al. (1986)
Oncorhynchus nerka	<0.2	
Oncorhynchus kisutch	<0.2	
Oncorhynchus tshawytscha	0.8	Wilson et al. (1987)
Coregonus clupeaformis	0.4	Bernatchez and Dodson (1990b)
Coregonus artedii	1.0	Bernatchez and Dodson (1990a)
Galaxias truttaceus	0.9	Ovenden and White (1990)

lotypes separate into three main groups: an A group which predominates in the eastern Great Lakes drainage, a B group predominant in the central region and a C group in the west. This distribution appears to reflect the recolonization of Canadian lakes from three separate glacial refugia. By contrast, allozyme data revealed only a western group whose distribution corresponded with that of group C, and a second group whose range encompassed the whole of the Great Lakes drainage (Ward et al. 1989). Thus, mtDNA retained a history of the isolation of walleye in an Atlantic refugium, whereas nuclear DNA did not. Similarly, the allopatric origin of sympatric populations of lake whitefish (*Coregonus clupeaformis*) in the Allegash Basin was detected by mtDNA analysis but not by allozymes (Bernatchez and Dodson 1990b).

Similar examples of mtDNA dichotomies have been noted for marine environments. Populations of *Fundulus heteroclitus* along the Atlantic coast of North America show a step cline in mtDNA haplotype frequencies, but generally exhibit smooth clinal variation in allele frequencies and morphology (González-Villaseñor and Powers 1990). Mitochondrial DNA discontinuities have also been observed in several marine invertebrates (Saunders et al. 1986; Reed and Avise 1990) again contrasting with the near uniformity of allozyme frequencies.

Population bottlenecks associated with the Pleistocene glaciation appear to have had severe impacts on the extent of both haplotype diversity and divergence in many temperate zone fish populations. Bernatchez et al. (1989) compared the levels of mtDNA variation in whitefish, *Coregonus clupeaformis* from Hudson–James Bay region in North America and *C. laveratus* from the Bothnian Gulf in Europe. These species have similar abundances, life histories and potential for intra- and interpopulational gene flow, and may represent allopatric populations of the same taxon. *C. clupeaformis* survived the Pleistocene in three refugia, only one of which colonized Hudson– James Bay, while much of the range of *C. laveratus* was unglaciated. As expected, *C. clupeaformis* exhibited far lower levels of mtDNA diversity than *C. laveratus*. Similarly, Bernatchez and Dodson (1990a) found higher haplotype diversity and divergence in cisco, *C. artedii*, than *C. clupeaformis* populations from Hudson–James Bay. They attributed this difference to cisco having recolonized the area from two separate refugia, compared to the origin of the whitefish from a single refugium.

Reduced mtDNA variation among fishes affected by glaciation is not confined solely to the Northern Hemisphere. Ovenden and White (1990) found that landlocked populations of the anadromous fish, *Galaxias truttaceus*, in lakes on the recently glaciated Central Plateau of Tasmania also showed little mtDNA diversity. They postulated that this was due to a transitory-bottleneck possibly induced by selection for life-history characters essential for survival in the lacustrine habitat.

Stock Discrimination

Allozyme analyses have been successful in stock discrimination of many fish species (Allendorf et al. 1987), but in some species comprehensive allozyme studies have failed to reveal significant genetic variation (Todd 1981; Leary and Booke

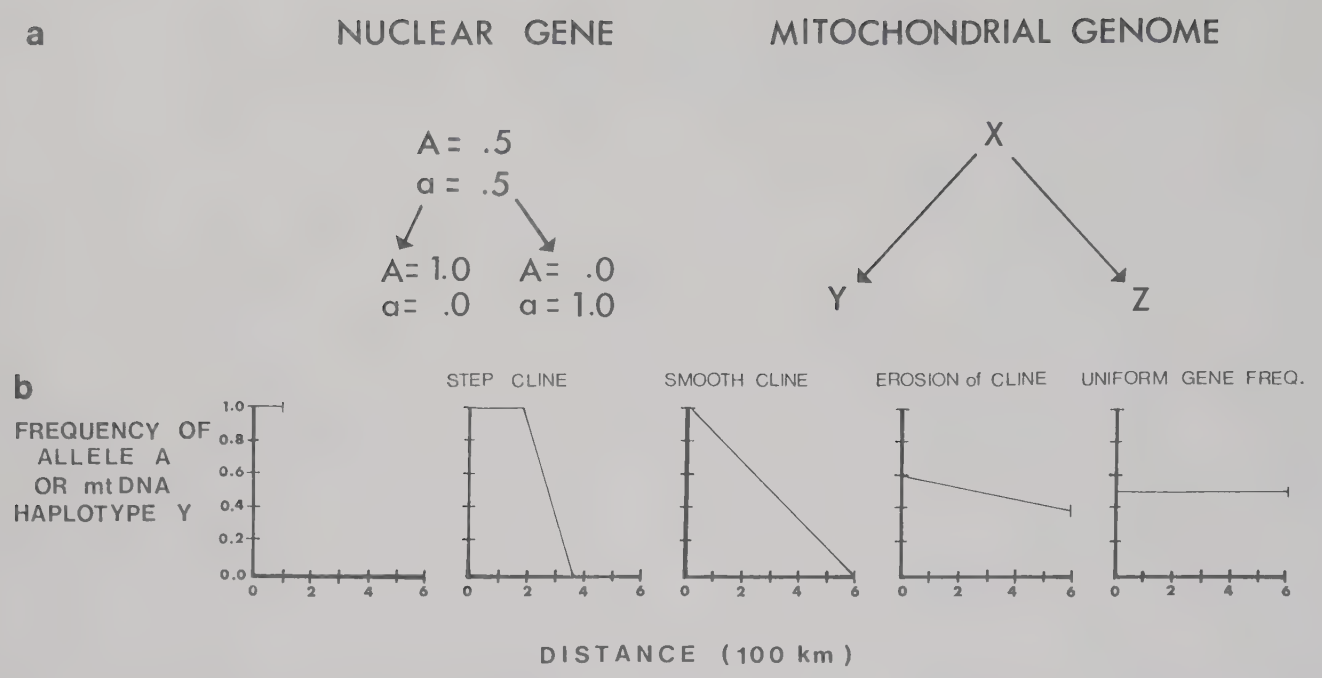

FIG. 2. (a) Genetic divergence at gene loci in the nuclear and mitochondrial genomes as a result of the fragmentation of a single population into two subpopulations. (b) The subsequent erosion of divergence through time (graphs from left to right) in populations along an arbitrary 600 km transect as a result of secondary fusion. The pattern of erosion is similar for both genomes, but at the end of the process the population retains two distinct mtDNA haplotypes, providing a record of their past isolation.

1982). It is now apparent that there is substantial mtDNA variation in many fish species and that this variation can serve as a basis for stock discrimination (Ferris and Berg 1987; Gyllensten and Wilson 1987; Bermingham 1990). It is, however, also important to consider the limitations of mtDNA-based stock recognition. Mitochondrial DNA evolves at a rate of 2% per million years (Brown 1983), or 300 bp per million years assuming a 15 000 bp long molecule. If the entire molecule is surveyed this corresponds to 3 bp substitutions per 10 000 yr. Therefore, even with complete isolation, populations which have colonized habitats since the end of the Pleistocene will show little divergence. Moreover, as most mtDNA studies are based on surveys of 3–5% of the genome, the chance of identifying divergence is further attenuated. It is hence unrealistic to expect to be able to differentiate stocks in nearby river or lake systems on the basis of divergence which has arisen since their relatively recent colonization. Fortunately, the ability to discriminate stocks does not rest solely on divergence which postdates isolation, but instead may also be based on preexisting mtDNA polymorphisms (Bernatchez et al. 1989; Ward et al. 1989; Bernatchez and Dodson 1990a). Such divergence arises as a consequence of sampling effects associated with population founding. In the extreme case, where individual populations originate from a single, or few females, stochastic lineage extinction (Avise et al. 1987a) may lead to their fixation for different haplotypes, thus permitting unambiguous discrimination of the stocks.

The value of shifts in mtDNA haplotype frequency for stock discrimination has been clearly shown in a number of studies. Wilson et al. (1987) were able to discriminate chinook salmon from Alaska and British Columbia, while Bentzen et al. (1989) were able to discriminate among populations of American shad along the Atlantic coast of North America. Ward et al. (1989) showed that, consistent with theoretical expectations (Nei and Tajima 1981; Birky et al. 1983), mtDNA data were more effective for discrimination of walleye stocks than were allozyme data; 37% of the total variation among walleye mtDNA haplotype frequencies could be attributed to interpopulation variation, whereas only 10% of allelic frequency differentiation was linked to interpopulational variation. Bernatchez and Dodson (1990a) were able to identify three distinct genetic pools in anadromous cisco collected from James–Hudson Bay rivers. Further evidence of structuring in Hudson Bay was suggested by the presence of unique haplotypes in stocks from specific rivers. There also appears to be sufficient site-specific mtDNA variation among eastern North American populations of lake whitefish (Bernatchez and Dodson 1990b) to suggest that some population discrimination is possible. Some studies have failed to detect such genetic divergence, but in most cases sample sizes were inadequate to provide any basis for meaningful stock discrimination.

Neointroductions

In previous sections, we have noted that the current distributions of many fish species reflect their recolonization of areas affected by the Pleistocene glaciation, and as such can be considered as "Paleointroductions." In the present section, we consider the implications of more recent introductions of fish by man. The genetic implications of fish introductions have been recently discussed by Ferguson (1990), who outlined the problem of transfers of fish (movement of fish from one location to another within the range of the species). This problem has been largely overlooked by fisheries managers, yet the genetic consequences of such transfers may be serious (Philipp 1991).

The present review has made clear that many fish species show geographical differentiation in the distribution of mtDNA

haplotypes. While these mtDNA differences themselves are probably of little adaptive significance, they do indicate an historical separation, which one would surmise might be accompanied by local adaptation of the nuclear genome. Such local adaptations may be destroyed by the introduction of "foreign" (i.e. transplanted) fish, setting the stage for the loss of the resident population.

In a number of fish species, the identification of genetically distinct stocks has been complicated by recent stocking programs. For example, Ovenden et al. (1988) suggest that the introduction of *Gadopsis marmoratus* into southern Tasmania has complicated the resolution of evolutionary relationships in this species. Bermingham and Avise (1986) have similarly suggested that a disjunct mtDNA pattern in *Lepomis gulosus* might have been due to stocking of fish from another drainage. Analysis of *Stizostedion vitreum* populations in the U.S., where supplemental stocking is a common management practice, has identified fish with mtDNA types not ordinarily expected in the area (Billington et al. 1992). Furthermore, examination of stocked populations from known origins confirmed that such populations show similar proportions of mtDNA haplotypes as their source populations (Billington et al. 1992).

Many questions concerning the effects of stocking and other management practices on fish populations can be examined by the use of genetically marked fish. The establishment of nonlethal sampling techniques permits the establishment of lineages with known mtDNA haplotypes (Billington and Hebert 1990). Such mitochondrially marked fish could be used for conducting experimental stocking studies. For example, different strains of fish marked with mtDNA tags could be stocked in a lake and their relative success evaluated. Alternatively, although we have discussed the possible adverse genetic consequences of such an experiment, mitochondrially marked fish could be stocked into systems where natives are known to have a different haplotype and their establishment relative to the native fish determined. If females of these stocked fish become established and reproduce, their mtDNA haplotype will be perpetuated due to maternal inheritance, even if they breed with native males, permitting a multi-generation assessment of their success.

If mtDNA markers are to be used for assessing the success of fish introductions, it is important to survey mtDNA variation in both natural populations and existing broodstocks. A number of studies have begun the assessment of mtDNA variation in hatchery broodstock. For example, Palva and Palva (1987) found restriction site variation among four Finnish broodstocks of rainbow trout, and Grewe and Hebert (1988) found considerable mtDNA variation among nine lake trout broodstocks. Palva et al. (1989) found unique restriction fragment patterns for two hatchery stocks of Atlantic salmon, while Hynes et al. (1989) found diagnostic fragment patterns in both wild and hatchery brown trout stocks. Gyllensten and Wilson (1987) found fixed genetic differences among three hatchery stocks of rainbow trout and two hatchery stocks each of brown trout, Atlantic salmon and cutthroat trout. Gyllensten and Wilson (1987) noted that the lack of variation in hatchery stocks might typically be a result of their origin from a very few females. However, sample sizes in their study were small (3–5 fish per stock) and may have failed to detect all of the variation present.

The work so far complete makes it clear that many broodstocks are easily discriminated on the basis of existing mtDNA differences. In those fisheries which rely solely upon stocking programs, this is all the information which is required for assessment of differential growth and survival in a mixed stock fishery. In other cases, however, stocking programs act to augment resident fish stocks and thus, discrimination of stocked and resident fish requires an assessment of natural mtDNA diversity. As might be expected, broodstocks are often fixed for common haplotypes making discrimination of stocked and resident fish impossible. There is, however, the opportunity to establish new broodstocks marked with rare mtDNA haplotypes which would permit discrimination of hatchery and wild fish. Mitochondrial DNA markers could also provide a method for monitoring the frequency of escapees from fish farming or cage culture operations in wild stocks (Hynes et al. 1989; Skaala et al. 1990).

Perspective

This review has largely concentrated on mtDNA diversity in temperate fish as little attempt has been made to study mtDNA diversity in tropical fishes. There is generally less information on marine than freshwater fish, although as a recent review (Ovenden 1990) shows, mtDNA analysis is also being used in studies of marine stock identification. It is evident that mtDNA diversity is ubiquitous in most fish species. The study of mtDNA diversity is providing new insights into phylogenetic relationships at higher taxonomic levels, but is poised to make an even greater contribution to the analysis of genetic diversity in single species. There is growing evidence that local stocks can often be discriminated, even in habitats colonized since the end of the Pleistocene glaciation, as a result of stochastic shifts in haplotype frequencies. This has important implications for fisheries managers as it suggests that transfers of fish may be detrimental to locally adapted stocks. Surveys of mtDNA diversity have detected the presence of large numbers of rare haplotypes in most species, providing a basis for the development of genetically marked lineages. These rare haplotypes can be used as genetic markers, and as they are transmitted by females to their offspring, the persistence of stocked mtDNA haplotypes can be followed. This is likely to be of particular value in fisheries which rely upon the supplemental stocking of fish for their maintenance, and for monitoring escapees from aquacultural operations. Moreover, such markers will be important in conducting experiments to monitor the genetic effects of transferring fish among populations. This range of applications make it clear that the analysis of mtDNA diversity has much to contribute to fisheries management.

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Rapid mtDNA Sequence Analysis of Fish Populations Using the Polymerase Chain Reaction (PCR)[1]

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The polymerase chain reaction (PCR) is a relatively new technique allowing the enzymatic amplification of selected genes to produce quantities sufficient for the determination of nucleotide sequences. We have compared sequences of several genes from the mitochondrial genome of six salmonid species. PCR analysis of protein coding genes provides sufficient resolution for determining relationships among species, or among isolated populations. Examination of more variable regions, such as the control region of the mitochondrial genome, will be required for other intraspecific comparisons.

La réaction en chaîne à la polymérase (RCP) est une technique relativement nouvelle qui permet l'amplification enzymatique de gène sélectionnés pour en produire des quantités suffisantes pour faire la détermination des séquences de nucléotides. Nous avons comparé les séquences de divers gènes du mitogénome de six espèces de salmonidés. L'analyse après RCP des gènes de codage des protéines donne une résolution suffisante pour déterminer les relations au sein des espèces ou entre populations isolées. L'examen de régions plus variables, comme la région de contrôle du mitogénome, sera nécessaire pour les comparaisons entre espèces.

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The polymerase chain reaction (PCR) is a relatively new technique that permits the enzymatic amplification of selected DNA sequences, from miniscule initial amounts, to sufficient quantities for direct sequencing or cloning (Mullis et al. 1986). It is a technique that is revolutionizing DNA sequence analysis for population and evolutionary studies.

The principal advantages of PCR are:

1) It is very rapid. Once the technique has been optimized for a specific targeted sequence, tissue samples can be extracted and the DNA amplified and sequenced (i.e., 200 or more contiguous base pairs identified) in less than a week. To obtain comparable nucleotide samples using restriction analysis or standard cloning and sequencing requires months of work.

2) It can utilize tiny quantities of tissue. A few milligrams of tissue or a small quantity of blood (Kawasaki 1990) can provide sufficient starting material for PCR sequence analysis. Thus it can be used even when it is not possible to sacrifice the animals for tissue.

3) It is extremely robust. Even if the tissue is in poor condition, with macromolecules broken up or partially degraded, PCR is sufficiently selective to amplify only those fragments of the desired sequence that are intact. Tissue that has been frozen, dried, or preserved in ethanol or formalin (Dubeau et al. 1986; Wright and Manos 1990) may contain sufficient intact DNA for PCR amplification and direct sequencing. Thus our museums and collections are now repositories of tissue that can be exploited for DNA sequence information (Pääbo et al. 1989).

In this paper I look first at the technique itself, then examine the animal mitochondrial DNA (mtDNA) genome to see how PCR can be applied to its study. Finally I will look at data we have obtained on Salmonids that will enable us to optimize the information obtained using the technique for studies at the population, species or even higher phylogenetic levels.

Polymerase Chain Reaction

PCR uses DNA polymerase extracted from the thermophilic bacterium, *Thermus aquaticus*, to replicate DNA fragments from partially purified DNA samples (Saiki et al. 1988). The polymerase is called *Taq polymerase*, using the first letters of the genus and species to identify the bacterial source. As is the case for all DNA polymerases, Taq polymerase cannot actually initiate a new DNA strand; it can only extend an existing strand. A different enzyme, primase, normally initiates short nucleotide strands at various points in the genome, to serve as primers for the polymerase. For PCR, no primase is used. Instead, short single stranded nucleotide chains (oligonucleotides) are provided as primers for the polymerase. These primers, by virtue of the property of base pair specificity of DNA, will bind to single stranded DNA only where the sequence is a very close complementary match. Thus the primer sequences can target the polymerase action to specific starting points. It is now possible to purchase custom made oligonucleotides (typically 20 or more nucleotides in length) of any desired sequence, targeting any selected region of the genome. By constructing two such primers, bracketing the desired gene, and on opposite strands, complete double strand copies of the desired sequence can be made.

The process is depicted in Fig. 1. It is assumed that the sequence on either side of the desired gene is known, and that

[1]This paper forms part of the Proceedings of the Ecological and Genetic Implications of Fish Introductions Symposium (FIN) convened at the Great Lakes Institute, University of Windsor, Ontario, Canada, May 17–19, 1990.

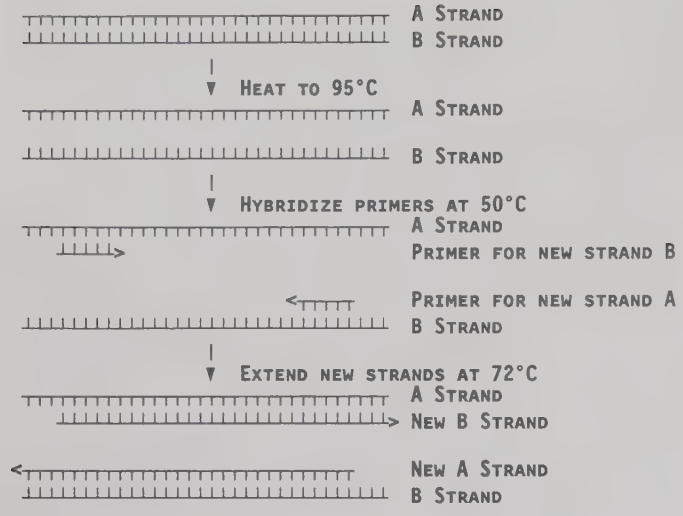

FIG. 1. PCR amplification of a short stretch of DNA. The strands of the DNA double helix must first be separated by heating to 95°C. The mixture is cooled to allow the primers to locate and bind to the targeted sequences. The polymerase then extends each primer into new strands, doubling the number of copies of the gene, between and including the primers themselves. The entire process is repeated 25 to 30 times, yielding as much as a 2^{30}-fold amplification of the gene.

primers have been constructed to direct DNA synthesis through the gene and past the other primer. The double stranded DNA is melted apart by heating to 95°C. (Taq polymerase, derived from a thermophilic bacterium, survives this process.) The mixture is cooled to allow binding of the primers. The primers, being small and in high concentration, quickly find the targeted sequence. The mixture is then heated to 72°C, the optimal temperature for Taq polymerase, for replication to occur. Even though the initial sample is a complex mixture of DNA sequences, only regions with bound primers can be replicated. The temperature cycle is then repeated 25 to 30 times, yielding an exponential increase in the number of copies of the targeted sequence.

In summary, the selectivity is achieved by the base pairing specificity of the primer sequences, while the amplification and purification results from the exponential increase in copy number resulting from the replication process. Sufficient quantities of a single sequence are produced to use in standard sequencing procedures.

The Mitochondrial Genome

The procedure described above seems to pose a problem: you must already know the flanking sequences (defining the primer sequences) in order to amplify and determine the internal sequence. For population studies, and in particular, in the study of mtDNA gene sequences, this problem is easily circumvented (Kocher et al. 1989). It is only necessary to find sequences that are evolutionarily conserved, bracketing regions that vary. The primers so defined can then be used in routine population surveys. The animal mitochondrial genome is particularly favorable in this regard. It is highly conserved in its genic content, and to a lesser extent, in gene organization.

Figure 2 gives the gene content and organization of the mitochondrial genome of humans (Anderson et al. 1981). The gene organization is identical in the frog, *Xenopus*, and as far as is currently known, in fish as well (Moritz et al. 1987). There are

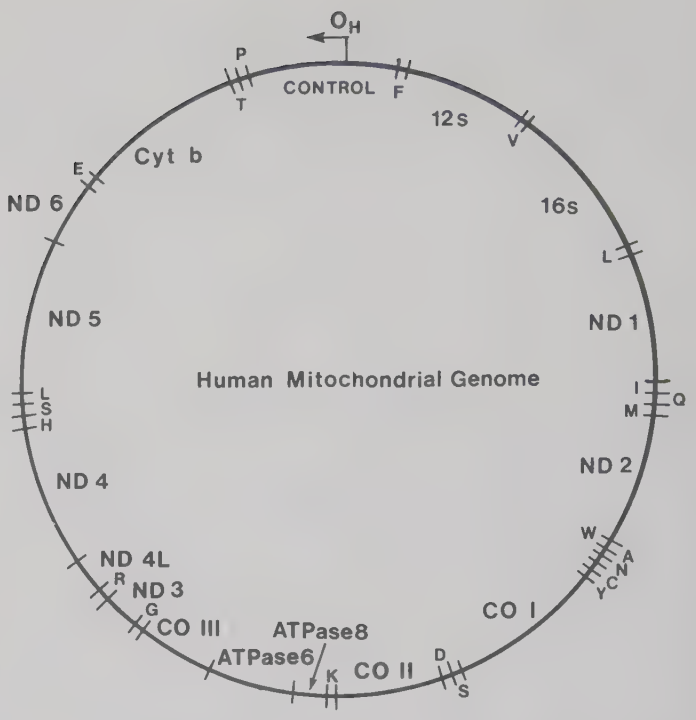

FIG. 2. Gene content and organization of the human mitochondrial genome. Single letters are the designations for the 22 tRNA genes; 12s and 16s refer to the two rRNA genes; the Control region and replication origin (O_H) are also indicated. The other labels indicate the 13 protein coding genes: ND = NADH Dehydrogenase subunits 1–6; CO = Cytochrome Oxidase subunits 1–III; Cyt b = Cytochrome b. Genes labelled inside the circle are transcribed in a clockwise direction. Those outside are transcribed counter-clockwise. Note that the tRNA genes tend to flank the protein coding regions. (From Anderson et al. 1981.)

13 protein coding genes, 22 tRNA genes, two rRNA genes and a non-coding control region (or D-loop). Empirical evidence shows that these genes have a hierarchy of levels of conservation. The tRNA and rRNA genes have sequences sufficiently conserved to define primers that can be used on any vertebrate species, or in some cases, apparently on any animal species (Kocher et al. 1989). The protein coding genes show variation, particularly at the third codon position, among individuals of a species (Beckenbach et al. 1990) and among closely related species (Thomas and Beckenbach 1989). By determining the DNA sequence of a protein coding gene, we can derive the inferred amino acid sequence of the protein. Amino acid substitutions change at a rate suitable for phylogenetic studies at the genus, family and higher levels of relationships. Finally, the most rapidly evolving region is the control or D-loop region (Moritz et al. 1987). Sequence analysis of this region promises to yield sufficient variability among lineages to give high resolution at the population level.

It is clear from the organization of genes (Fig. 2) that primers based on the conserved tRNA or rRNA genes can be used to amplify either the protein coding genes or the control region, depending on the degree of resolution desired. We have successfully amplified part of the control region of stickleback fishes, using primers defined on the basis of the known human mtDNA sequence (Anderson et al. 1981; Kocher et al. 1989). We have also successfully amplified essentially the entire control region from salmonids and stickleback fishes, using primers

TABLE 1. Intraspecific sequence variation (%) of mtDNA in some salmonids. Restriction analysis estimates sequence divergence based on sampling of the entire genome. Sequencing estimates are based on sequence of a 2214 base pair region coding for four proteins and two tRNA genes.

	Restriction analysis	Sequencing
Rainbow trout	0.5[1]	0.25[2]
Sockeye and coho salmon	<0.16[3]	
Chinook salmon	0.5[3]	

[1]Wilson et al. (1985).
[2]Beckenbach et al. (1990).
[3]Wilson et al. (1987).

based on the sequence from the white sturgeon (Buroker et al. 1990; Jim Brown, personal communication).

Analysis Strategies for Salmonids

We have now obtained sufficient sequence information on Pacific salmonids to develop strategies for PCR analysis at virtually any desired level of resolution. Table 1 gives the observed intraspecific sequence variation in several salmonid species, using two methods of analysis: restriction analysis and sequencing of a cloned fragment. The restriction analysis was based on about 400 nucleotides sampled from each individual (Wilson et al. 1985, 1987). The sequencing of rainbow trout is based on the complete sequence, from six individuals, of a 2214 base pair fragment, coding four proteins and two tRNAs (Beckenbach et al. 1990). Since sequencing of long stretches of DNA is a very tedious procedure, five of the six individuals chosen were already known to be different, based on prior restriction analysis work. Thus the observed divergence of 0.25% probably represents an over-estimate of the actual variation present in protein and tRNA coding regions.

If one takes into account the frequencies of observed clonal lines in the intraspecific comparisons, and the number of nucleotide differences between separate clonal lines, the actual sequence divergence observable between random individuals within a single population, based on either restriction fragment analysis or sequence information is generally less than 0.5% (Wilson et al. 1987; Beckenbach et al. 1990). This empirical result suggests that neither restriction analysis nor sequencing of coding regions provides sufficient resolution for intraspecific comparisons.

One apparent discrepancy can be seen from Table 1: restriction analysis of rainbow trout gives a much higher estimate than does sequencing, despite the fact that the sequencing data probably represents an over-estimate (see above). This discrepancy is probably real, resulting from the fact that restriction analysis samples the entire genome, including the non-coding control region. The control region appears to evolve much faster than the coding regions (Moritz et al. 1987). This observation suggests that a study of the control region may provide sufficient resolution for population level analysis. We have begun a test of this hypothesis, examining the region in cutthroat trout using PCR and direct sequencing. PCR amplification using primers based on the $tRNA^{pro}$ (P in Fig. 2) and a conserved block of sequence near the other end of the control region amplifies a fragment of about 1 200 base pairs. Direct sequencing of three individuals showed apparent differences in sequences of all three (unpublished results). Additional work will have to be done to determine if a quantitiative estimate of the sequence variation in this region can be obtained.

TABLE 2. Interspecific sequence variation (%) of mtDNA in some salmonids.

	Restriction analysis	Sequencing
Chinook — Coho	2.66	6.8
Rainbow — Coho	3.04	12.6
Rainbow — Chinook	3.18	13.6
Rainbow — Sockeye	5.08	15.4
Chinook — Sockeye	5.28	14.9
Rainbow — Pink	7.51	16.3

NOTES: Estimates from sequencing are corrected for multiple replacements (see Thomas and Beckenbach 1989).
[1]Thomas et al. (1986).
[2]Thomas and Beckenbach (1989).

Table 2 shows a comparison of restriction analysis and sequencing for selected species pairs of salmonids. The interspecific divergence is an order of magnitude greater than the intraspecific variation observed in these species. In contrast to the intraspecific comparisons, the estimates based on restriction analysis are lower than those based on sequence of a 2214 base pair coding region. It is likely that restriction analysis is simply missing a large number of multiple events occurring at the variable sites, particularly those in the control region. It is clear from comparison of the sequences of these species (Thomas and Beckenbach 1989), that amplifying protein coding regions would provide excellent resolution for species-level analysis.

Prospects for Routine Stock Identification

Routine stock identification and large-scale surveys require processing of large numbers of individuals. The methods described in this paper are simpler than standard cloning and sequencing methods, and provide much more information than can be obtained by restriction analysis. They are nevertheless too expensive and too technically demanding for large-scale routine surveys. It may, however, be possible to exploit sequence information obtained from PCR and sequencing surveys, to develop stock identification probes that can be applied quickly and inexpensively to large sample sizes. The key is to design oligonucleotides for use as probes rather than primers. Each probe is constructed to be a perfect match to one of the sequences, but with one or more mismatches to each of the other sequences. The probes can be labelled either with a coloured dye, or with a radioactive nucleotide. Such probes, once developed, could be easily applied in routine surveys to identify fish carrying those specific sequences. Methods are available, using dot blots of crudely extracted DNA, which do not require PCR, sequencing or gel electrophoresis (Miller and Barnes 1986).

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Implications of Introduction of Transgenic Fish into Natural Ecosystems[1]

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Production of transgenic fish has increased in scope, aimed at improving performance traits in economically important species or at creating model systems for basic biological problems. A variety of transgenic phenotypes will become possible as more genes are cloned and characterized. Categories of altered phenotypes include modified: metabolic rates; tolerance of physical factors; behavior; resource or substrate use; and resistance to disease, parasitism, or predation. Ecological impacts of transgenic fishes are uncertain but will depend primarily on their altered phenotypes and secondarily on the scale and frequency of their introduction into ecosystems. Production of ecologically noxious transgenic types is possible, because many fish varieties readily disperse and persist in aquatic ecosystems, are fit in natural settings, interact substantially with other organisms, and play a role in ecosystem processes. Releases of transgenic fishes may impact aspects of fisheries management. Because future uses of transgenic fish in commercial aquaculture or in stocking of natural waters are contemplated, interdisciplinary teams of fisheries biologists, ecologists, and resource managers must develop integrated approaches to assessing risks of ecological impacts. The current situation of uncertainty demands caution in expecting "safe" uses of transgenic fishes.

La production de poissons transgéniques, visant à améliorer les caractéristiques de rendement chez des espèces d'importance économique ou à créer des modèles conçus pour étudier des problèmes biologiques fondamentaux, a pris de l'extension. Il sera possible de produire une variété de phénotypes transgéniques à mesure que d'autres gènes seront clonés et caractérisés. Il existe diverses catégories de phénotypes modifiés : taux métabolique; tolérance à des facteurs physiques; comportement; utilisation des ressources ou des substrats; résistance à la maladie, au parasitisme ou à la prédation. Les effets écologiques de l'introduction de poissons transgéniques sont incertains, mais ces effets dépendront premièrement du type de phénotypes modifiés et, deuxièmement, de l'importance et de la fréquence de l'introduction de ces poissons dans les écosystèmes. La production de types transgéniques nuisibles sur le plan écologique est possible, car de nombreuses variétés de poissons se dispersent et survivent facilement dans l'environnement, sont adaptées aux conditions naturelles, interagissent de façon importante avec d'autres organismes et jouent un rôle dans les processus écosystémiques. La libération de poissons transgéniques peut avoir des effets sur certains aspects de la gestion des pêches. Comme on prévoit utiliser dans l'avenir des poissons transgéniques en aquiculture commerciale ou pour l'empoissonnement d'eaux naturelles, il faut que des équipes interdisciplinaires formées de biologistes des pêches, d'écologistes et de gestionnaires des ressources élaborent des stratégies intégrées pour évaluer les risques d'effets écologiques. L'incertitude actuelle exige que l'on fasse preuve de prudence face à l'utilisation sans danger des poissons transgéniques.

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We are witnessing times of great irony for genetic diversity. On the one hand, the planet is experiencing the first anthropogenically induced mass extinction, in which one-quarter to one-half of the earth's species will become extinct in the next 30 yr (Cairns 1987; Wilson 1989; Holden 1990). Only recently has this unprecedented consequence of human activity commanded world attention and concern from politicians, businessmen, and citizens, in addition to ecologically oriented biologists and environmental advocacy groups, the traditional supporters of natural diversity. Numerous texts review the detrimental consequences of this mass extinction for ecosystem stability, global biogeochemical cycles and life support systems, agriculture, industry, and overall quality of life in human societies (e.g., Norton 1986; Wilson 1988; Oldfield 1989). On the other hand, new recombinant DNA methods have greatly expanded the plans of humans to design the genetic makeup of organisms to their specifications. Human-prepared combinations of DNA are inserted into the genome of a host species, with the intent of modifying a targeted trait. Relative to the host, these novel genetic constructs may contain DNA from the same, closely related, distantly related, or unrelated species, or any combination thereof.

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At the same time that human cultures are destroying vast and diverse collections of natural genetic information accumulated by the master librarian of evolution, genetic tinkerers promise that a better world will emanate from their insertions of novel DNA constructs into economically important species of microbes, plants, and animals. This process is better described as genetic "tinkering" than "engineering" because it is currently impossible to predict or explain all the influences of inserted genes on the development, physiology, behavior, and ecology of a modified organism (Regal 1986).

Connections between these two spheres of human activity, mass extinction and genetic tinkering, are rarely considered. First, raw material for creation of new genetic constructs comes from the diversity of naturally occurring genes, which is rapidly diminishing. For example, the list of threatened, endangered, or extinct fish species grows steadily (e.g., Williams et al. 1989; Miller et al. 1989), and intraspecific genetic diversity continues to decline (Berst and Simon 1981; Nelson and Soulé 1987). Second, even with unforeseen advances in technology, long lists of different transgenic organisms will neither replace the vast diversity of naturally occurring organisms nor the goods and services they contribute to ecosystems and human societies. Third, introductions of some transgenic organisms into natural ecosystems could trigger ecological perturbations (Tiedje et al. 1989; Kapuscinski and Hallerman 1990), some of which could actually exacerbate the current trend of mass extinction. Genetic engineering of fish, which has increased dramatically in the last decade, must be examined in the context of these three issues regarding mass extinction.

For fish, genetic engineering can refer to both ploidy manipulations (Thorgaard 1986) and gene transfer (Kapuscinski and Hallerman 1990). In this paper, we focus on transgenic fish in a review of ecological concerns about introducing them into natural environments. We also discuss related implications for fisheries management policy.

Technical Background

Transgenic fish contain copies of novel genetic constructs introduced into their chromosomal DNA by modern genetic techniques. These constructs, or spliced genes, consist of structural genes (DNA sequences encoding a specific protein product) linked to regulatory sequences (DNA sequences necessary for successful expression of the structural gene). Production of transgenic fish has grown rapidly in the last 5 yr, involving at least 22 research labs in 14 countries (Hallerman et al. 1989) and at least 14 fish species (Kapuscinski and Hallerman 1990; Moav et al. 1992). The impetus for such work has been to improve desirable performance traits in economically important stocks or to create model fish systems for investigating basic questions about genetic regulation, physiology, behavior, and other aspects of vertebrate biology (Powers 1989). While the former aim sets the stage for most of the ecological concerns, the latter represents a powerful laboratory tool for researching mechanisms in vertebrate biology. Noakes (1986), for instance, pointed out the value of gene transfer for testing hypotheses about relationships between single genes and fish behavior in experimental settings.

Diversity of types of transgenic aquatic organisms is likely to increase as techniques of gene transfer improve and the variety of genes available for insertion increases (Kapuscinski and Hallerman 1990). While the focus to date has been on genetic transformation on fish, production of other transgenic aquatic organisms has been reported, including frogs (Etkin and Pearman 1987) and sea urchins (Flytzanis et al. 1985). An example of future opportunities is the finding that vertebrate growth hormone enhanced growth of abalone (Morse 1984). Transfer of growth related genes is likely to yield growth enhancement in this economically important invertebrate.

Currently, little quantitative information is available on the magnitude or direction of changes in primary traits affected by transgene expression in fish. The small database, however, does indicate presence of much apparently transgene-induced phenotypic variation in first generation transgenic fish (MacLean et al. 1987; Zhang et al. 1990; Gross et al. 1992). Much of this variation presumably reflects variation among genotypes for integrated transgenes, including mosaicism (Kapuscinski and Hallerman 1990). Two or more generations of selection of transgenic fish will be necessary to produce lines showing more homogeneous transgenic genotypes and expression, and desirable performance in other important traits. According to principles of molecular genetics (Old and Primrose 1985) and quantitative genetics (Falconer 1989), the expression of targeted traits in a transgenic individual will be determined by the: structural gene and regulatory elements of inserted gene constructs; integration sites and number of copies of intact transgenes; overall genetic background of the host genome; species-specific developmental dynamics; and environmental influence on gene expression.

Little or no quantitative information on changes in traits genetically or phenotypically correlated to the trait targeted by inserted transgenes is currently available for transgenic fish. This is due in part to the infancy of investigations with groups of fish that are homogeneously transgenic (Kapuscinski and Hallerman 1990), and in part to the tendency for genetic engineering research to be so goal-directed that it is not biologically detailed. Although the number of reports are increasing regarding growth enhancement in transgenic fish containing extra growth hormone genes, (Zhu et al. 1986; MacLean et al. 1987; Yenikolopov et al. 1989; Zhang et al. 1990; Gross et al. 1992), quantitative determinations of averages and variances for age at sexual maturity, fertility, food conversion, general disease resistance, or behavior of these fish are generally unavailable. Yet systematic study leading to enhanced expression of such traits over a lifetime would greatly influence the overall performance of transgenic fish.

Need for Assessing Risks of Impacts

Ecological risks of releasing transgenic fishes into natural waters will depend primarily on how their overall performance in a given environment is influenced by expression of inserted genes (Kapuscinski and Hallerman 1990). Despite current uncertainties about performance of transgenic fishes, various parties are already contemplating future uses of transgenic fishes in commercial aquaculture operations or in stocking of natural waters. Great interest in transgenic fishes, particularly by the commercial sector, makes it imperative that fisheries scientists, in collaboration with natural resources policy and regulatory organizations, develop interdisciplinary approaches to assessing risks of potential ecological and genetic impacts (Kapuscinski and Hallerman 1990a). Risk assessment protocols and methods must be flexible enough to allow incorporation of quantitative performance data as they accumulate.

Different types of transgenic fishes are likely to pose different types and degrees of ecological risk, depending on the over-

all phenotypic effect of the transgene and the normal ecological role of the host species (Tiedje et al. 1989; Kapuscinski and Hallerman 1990). We cannot rule out the possibility that some transgenic fishes will pose greater ecological risk than fishes whose endogenous genes have been simply recombined through artificial selection, hybridization of closely related species, or ploidy manipulations. Compared to these other types of genetically manipulated fishes, environmental introductions of some ecologically competent transgenic fishes are likely to pose greater ecological risk because "organisms with novel combinations of traits are more likely to play novel ecological roles, on averge, than are organisms produced by recombining genetic information existing within a single evolutionary lineage (Tiedje et al. 1989)."

Definition of Introduction into Natural Ecosystems

Differentiation among *containment, confinement*, and *release* (introduction) of genetically engineered organisms has ben extensively discussed for microbes, crop plants, and farm animals, and to a lesser extent for fish (USDA Cooperative State Research Service 1990; Mellon and Rissler 1990). Currently, the U.S. Department of Agriculture Animal and Plant Health Inspection Service is the responsible federal agency regulating field testing of transgenic fish in the United States (Hallerman and Kapuscinski 1992). This agency defines "containment" of transgenic organisms as a "term used to describe physical barriers that severely limit release of an organism to the environment," involving four Biosafety Levels of containment set by NIH guidelines (Purchase and Barbeito 1990). Under this definition, containment generally involves holding transgenic organisms within fully enclosed buildings. In contrast, confinement means that the movement of transgenic organisms "is confined within a designated outdoor environmental zone of control with designated borders or limits" (Purchase and Barbeito 1990). Release into the environment means "use of a regulated article outside the constraints of physical confinement of a laboratory. . . . . or other contained structure (Cordle and Langston 1989)."

Because USDA definitions of containment and confinement were designed primarily with terrestrial microbes, plants, and traditional agricultural animals in mind, a serious examination of their applicability to transgenic aquatic organisms is needed. For example, does containment, confinement, or release apply to holding transgenic salmon in completely indoor tanks, but with constant water flow discharged into an outdoor settling pond and then to surface waters? Does rearing transgenic carp in static-water, outdoor levee ponds pose more or less risk of accidental release than the former example? Answers to such questions depend primarily on the weakest link in any fish holding system, the water influent and effluent, and secondarily on other factors such as susceptibility to vandalism, flooding, storm damage, or predation (Kapuscinski and Hallerman 1990). Designation of a holding system as a containment, confinement, or release of transgenic fish must be based on the types of escape barriers in the water distribution system. Barriers could be physical (e.g., fine mesh screening around tank standpipes, sand and gravel traps), biological (e.g., heating of effluent water to lethal temperatures) or chemical (e.g., chlorination-dechlorination of effluent water).

For uses of transgenic fishes, we have previously outlined a spectrum of fish environments ranging from indoor research labs to natural aquatic ecosystems, and parallel ecological risks ranging from minimum to maximum risk (Kapuscinski and Hallerman 1990). The general and idealized nature of these series must be emphasized. Safety will come from intelligently following their content and not merely the letter of their language. A particular facility, whether indoor or outdoor, can be called 'confinement' only if its location, design, and management thoroughly minimize chances of release by all possible avenues. There is nothing magical about a building. A similar type of facility built and operated without careful consideration to all routes of escape might not fit under 'confinement' at all since it may lead to unintended release of some transgenic fish. Placement of a specific indoor or outdoor facility along the risk continuum should also be based upon the ecological vulnerability and value of nearby aquatic ecosystems. For example, we should have much higher standards for 'containment' if we are concerned about potential escape of transgenic fish into a natural wetland, especially if it contains rare endemic species, than if the concern is an artificially constructed reservoir with no outlets.

Ecological Implications

Rational and comprehensive risk assessment of impacts of introducing a particular type of transgenic fish into an ecosystem requires assembling interdisciplinary teams of scientists to examine attributes of the host species, the engineered trait, and the proposed introduction (Tiedje et al. 1989; Kapuscinski and Hallerman 1990). A gene can be completely characterized with regard to its DNA sequence, but the primary feature of transgenic individuals that will determine the types of ecological questions needing attention is characterization of the nature and magnitude of specific *phenotypic* changes elicited by expression of the transgenes. Based on these changes the evolutionary and ecological factors that should be addressed include: (1) the fitness of transgenic individuals; (2) natural interactions of the host species with other organisms and the related consequences of possible differences exhibited by transgenic conspecifics; (3) natural role of the host species in ecosystem processes and the related consequences of possible differences exhibited by transgenic individuals. Finally, (5) the scale and frequency of introductions into an aquatic ecosystem should be considered, as these will significantly influence likelihood of establishment, amount of genetic diversity available for recombination and genetic adaptation, and degrees of ecological risk.

Phenotypic Changes in Transgenic Fish

Possible phenotypic alterations in transgenic fish fall into at least five categories. These are changes in: metabolic rates; range of tolerance values for physical factors; behavior; resource or substrate use; and resistance to population regulating factors including disease, parasitism, or predation. A particular transgenic fish might exhibit changes in more than one category, and there may be overlap between categories and interactions between them.

Lack of knowledge about major genes controlling specific traits or unavailability of cloned DNA sequences currently limit the production of transgenic fish in any particular category. Some of these limitations will eventually diminish because of dramatic increases in the numbers of genes isolated and characterized from fishes and other organisms. Generally, genes cloned from other vertebrates may be biologically active in fish genomes, as has been observed in some experiments involving

mammalian growth hormone genes. They can also be used to probe for related genes in fish genomes (Kapuscinski 1990).

Metabolic rates

Numerous metabolic rates influence the value of one or more components of the balanced energy budget for an individual (Brett and Groves 1979). In turn, components of the energy budget, such as reproduction or growth, influence an individual's impact on nutrient and energy flows and other organisms in its environment. To date, most transgenic fish studies have involved growth hormone (GH) genes (Moav et al. 1992), with the intent of increasing growth rate, a composite of many physiological rates.

Tolerance of physical factors

Tolerance of physical factors such as temperature, pH, salinity, dissolved oxygen, or turbidity might be changed via transfer of specific genes into fish. Changes might occur in lethal limits or optimum values, thus shifting preferred habitats, seasonal effects on numbers or behavior, or extending the possible geographic range of a species. Current research on transgenic Atlantic salmon bearing antifreeze protein genes derived from winter flounder (Fletcher et al. 1988) falls into this category. The intent is to develop fish that survive supercooled seawater during winter rearing in net-pen aquaculture.

The possibility that salmonid fishes bearing inserted pituitary hormone genes might induce pleiotropic changes in a trait falling into this category is uncertain but worth considering. Growth hormone appears to have a role in osmoregulation in anadromous salmonids (Down et al. 1989; Powers 1989). During migration from freshwater to seawater, levels of GH are elevated, leading to an increase in Na^+ exclusion at the gills. The gene for prolactin, a hormone closely related to GH and also implicated in growth and osmoregulation (Powers 1989), has been cloned from fish (Song et al. 1988), providing an indirect option for alteration of osmoregulation by gene transfer.

Behavior

The transfer of specific genes has the potential to significantly affect fish behavior (Noakes 1986). Behaviors involved in reproduction, feeding, territorial defense, migration, or other life history features could be affected. Introductions of sufficient numbers of transgenic fish showing altered behavior could disrupt the normal course of life history events within a species or genetic stock, leading to changes in population dynamics or interactions with other species or genetic stocks, and possibly to destabilization of the aquatic community (Kapuscinski and Hallerman 1990).

Causal links between single genes and behavior have been documented to a limited extent in fish species and are likely to be common because they are widely established in every other kind of animal studied (Noakes 1986). In some cases, the phenotypic effect and adaptive significance of particular single genes are known, although influences of polygenes, pleiotropic gene interactions, and the environment may be also involved. A number of related life history features can change as a result of a single gene difference. Examples of single gene effects on behaviors with major ecological significance include: rainbow trout differing in lactate dehydrogense (LDH) phenotypes exhibit different swimming performances under different dissolved oxygen conditions (Klar et al. 1979); killifish (*Fundulus heteroclitus*) differing in LDH phenotypes show differences in swimming endurance and hatching time (DiMichele and Powers 1982); rainbow trout differing in phosphoglucomutase (PGM) liver isozymes exhibit different times of hatching and developmental rate, leading to differences in size and age of sexual maturity (Allendorf et al. 1983); and the onset of sexual maturation in *Xiphophorus* species is controlled by a single gene regulated by gonadotroph cells of the pituitary gland (Kallman 1983). These findings underscore the distinct potential for certain inserted genes to change ecologically significant behaviors in fish. Predicting the behavior of descendants of released transgenic fish, derived from matings among pure transgenic fish or with non-transgenic conspecifics, may be intractable due to polygenic and environmental influences, even in cases where a single gene has a major impact.

Resources or substrate use

Changes in resource or substrate use might occur through direct or indirect impact of transferred genes. Transfer of a gene whose protein product affects nutritional requirements of a fish would exemplify a direct impact. Gene insertions of this type have not yet been reported for fish, but may happen in the future by taking advantage of new knowledge of biochemistry of nutritional pathways. For example, certain dietary requirements are the consequence of lack of activity of one key enzyme in a key biochemical pathway. The action of the product of an inserted gene could complete the processing of a needed compound. It could also impede another pathway, leading to new dietary needs.

Indirect impacts falling into this category are exemplified by the potential for transgenic fishes bearing growth promoting transgenes to alter food webs. Compared to non-transgenic individuals, increases in their size at a given age may lead to increases in the size of their selected prey (Kapuscinski and Hallerman 1990). Based on studies of growth hormone administrations to fish, they could also have higher appetite (reviewed by Weatherley and Gill 1987). In some studies where food conversion was estimated, administration of growth hormone improved food conversion (Markert et al. 1977; Degani et al. 1985; Gill et al. 1985; Down et al. 1989). Thus, to assist risk assessment of ecological impacts of growth-enhanced transgenic fish, their appetite, food conversion, and prey-size selection need to be studied, preferably in the same or related experiments.

Resistance to disease, parasites or predation

Finally, certain genetic constructs might confer resistance to disease, parasitism, or predation in transgenic fishes. Although gene transfers of these types have not yet been reported for fishes, current biotechnological research with fish or other organisms is laying the necessary foundation for information on relevant major genes.

A number of lines of research may led to gene transfer to improve disease resistance of fish. Recombinant DNA vaccines are under development for infectious hematopoietic necrosis virus (IHNV), a fish rhabdovirus responsible for massive mortalities at government hatcheries and commercial aquaculture facilities for chinook salmon (*O. tshawytscha*) and rainbow trout (*Oncorhynchus mykiss*), and in populations in natural habitats of the North American northwest. Genetic constructs containing the glycoprotein gene of IHNV and inserted into *Escherichia coli* cells expressed a viral epitope of the IHNV glycoprotein (Gilmore et al. 1988). This glycoprotein elicited a neutralizing antibody and protective responses in vaccinated fish (Engelking and Leong 1989). These promising results could be applied to production of strains of salmonids resistant to IHNV by insertion of coat protein genes into their germ line.

In chickens, inserted envelope glycoprotein genes of subgroup A leukosis-sarcoma virus were expressed and gave a protective response, leading to formation of a resistant transgenic line (Salter 1988). Another opportunity for conferring disease resistance to fish via gene transfer lies in manipulating the major histocompatibility complex (MHC), a group of closely linked loci implicated in resistance to certain diseases in higher vertebrates (Chevassus and Dorson 1990). Although links between MHC polymorphisms and disease resistance have not yet been reported in fish, there is evidence for both MHC genes (reviewed by Chevassus and Dorson 1990) and expressed molecules (Stet et al. 1990). Because the vectors which carry the genes for transfer can accommodate no more than one, or perhaps two structural genes, insertion of novel MHC genes into fish would require techniques capable of transferring a group of structural genes. Preliminary steps towards this direction for fish were achieved by Thorgaard et al. (1985) and Disney et al. (1987) who created gynogenetic fish containing paternal chromosome fragments. Microinjection of chromosome fragments into zygotes would be another approach (Richa and Lo 1989). Chevassus and Dorson (1990) suggested additional future approaches to conferring disease resistance in fish by gene transfer.

Increased resistance of an aquatic organism to parasites or predators might be achieved by transfer of novel genes encoding for expression of specific defense compounds that are venomous or distasteful. Although we are unaware of research aimed at this kind of gene transfer, the foundation for it is being laid by accumulating evidence and chemical characterization of defense compounds in aquatic organisms (Halstead 1988; Scrimshaw and Kerfoot 1987; Olivera et al. 1990). Additionally, any category of phenotypic change in transgenic organisms that elicits a major deviation from the species' natural behavior or distribution in aquatic ecosystems could also effect an escape from parasites or predators.

Consequences of Phenotypic Changes

Phenotypic changes in one or more categories may modify life history patterns or spatial or temporal habitat distributions of transgenic fish compared to non-transgenic conspecifics. Consequently, transgenic individuals may have surprising ecological impacts due to their fitness, interactions with other organisms, role in ecosystem processes, or potential for dispersal and persistence (discussed in the following sections).

If any of the altered traits are subject to genotype-environment interactions (Falconer 1989), a particular transgenic fish will exhibit different overall performance in different aquatic ecosystems. This will only complicate the task of assessing risks of ecological impacts. Quantitative genetic studies have shown that genotype-environment interactions are common in fishes (Tave 1986).

Fitness of Transgenic Fish

Fish from artificially selected strains, in most cases, have not been domesticated enough to cripple their fitness (ability to survive and reproduce) in the wild. This is in sharp contrast to most other animal species used in gene transfer research. Transgenic lines of terrestrial livestock, such as pigs and feed lot cattle, would pose much less ecological risks because numerous generations of domestication have substantially lowered their fitness in natural environments. Whether transgenic fish introduced into natural settings exhibit high or low fitness will therefore depend on the influence of transgenes on fitness related traits. Introduced transgenic fish which initially display low fitness may simply become extinct, or they may develop increased fitness in response to natural selection. Rates of response to natural selection are heavily influenced by generation time and fecundity of a species. Many fish species have high fecundities and short generation times, allowing high rates of response to natural selection (Tave 1986).

Sterilization can reduce but not completely eliminate ecological risk associated with releases of transgenic fish. Significant introductions of sterile transgenic fish would still permit the occurrence of any non-genetic mechanisms for ecological impacts (Hallerman and Kapuscinski 1992). Existing technical limitations make it difficult to guarantee that every individual treated by one of various methods will be indeed sterile (Thorgaard and Allen 1987; Kapuscinski and Hallerman 1990a). In the event that sterile transgenic fish stocked into aquatic ecosystems had deleterious impacts, likely lags in detecting the problem would increase the risk of experiencing substantial or irreversible alterations before decisions were made to halt stocking programs (Kapuscinski and Hallerman 1992). Also, efforts to eradicate remaining fish and restore ecosystems will be greatly constrained by limitations or lack of technical and financial resources.

Interactions with Other Organisms

Interactions of the host species with other organisms will give some insight into potential risks of releasing transgenic individuals. Is the host species predatory, parasitic or mutualistic? What is the nature of its competitive and predator–prey interactions with other organisms in the aquatic community? Is it an introduced (exotic) species and, if so, has it been a pest in particular environments (Moyle et al. 1986; Kohler and Courtenay 1986; Welcomme 1988)?

Because of their altered phenotypes, transgenic fish of a particular species might display changes in interactions with other organisms. Both possibilities should be considered in ecological risk assessment. Additionally, three questions unique to interactions of transgenic individuals with other species should be considered. Do the overall phenotypes of transgenic individuals make them function ecologically like a noxious introduced species (reviewed in Kapuscinski and Hallerman 1990)? Would relatively large numbers of introduced transgenic individuals, via their altered phenotypes, act as agents of natural selection on other organisms in an aquatic community, and what would be the ecological consequences? Is there potential for fertile individuals to pass their transgenes to related species in the ecosystem? Because natural hybridization exists in a number of fish species (Turner 1984; Collares-Pereira 1987), this last question deserves careful examination.

Role in Ecosystem Processes

Transgenic individuals of keystone species could have a profound potential to impact ecosystems (reviewed in Kapuscinski and Hallerman 1990). Through their roles in nutrient cycling and energy flow, keystone or "singularly important" species influence values of parameters for these ecosytem processes (Connell 1975; Carpenter and Kitchell 1988). Because the trophic status of a fish species typically changes as it moves through different life stages, its lifetime role in ecosystem processes can be complex. This feature of most keystone species

will only complicate the task of assessing risks of the ecological impact of transgenic individuals.

Potential for Dispersal and Persistence

Ecological implications of releasing transgenic individuals will be heavily influenced by their abilities to disperse and persist in natural aquatic ecosystems. Ease of dispersal is almost a universal property of fishes. Dispersal is enhanced by a suite of dispersal agents existing in many natural aquatic ecosystems, including connections between water bodies and actions of humans, machines, birds, and other predators. A variety of fish species can survive adverse environmental conditions, such as dewatering, extreme variations in temperature, or major drops in dissolved oxygen. Transgenic individuals of these types of *host* species deserve special concern, as do individuals whose transgenes *confer* similar attributes.

Persistence of introduced transgenic fishes exhibiting ecologically novel phenotypes is particularly likely and problematic in lakes because of their "island" nature. By reviewing principles of island biogeographic theory and data on impacts of human-induced fish introductions, Magnuson (1976, 1988) concluded that lake faunas are especially susceptible to invasions of new species. Such invasions often dramatically alter and destabilize community structure via new species interactions. In turn, risks of local extinctions or global extinctions (in the case of endemic species) of lake species are increased. Also, fisheries managers are faced with increased uncertainty about response of a lake to management actions.

Risk assessment must include the possibility that persistence of introduced transgenic fishes may go undetected for several breeding generations before population sizes reach detectable levels. An example of this common trend for fish introductions is the population explosion of pink salmon (*O. gorbuscha*) in the Great Lakes (Kwain and Lawrie 1981; Emery 1981). After an introduction of approximately 21 000 fingerlings into Lake Superior in 1956, mature pink salmon were first reported in Minnesota waters of Lake Superior in 1959. The first six generations produced only small runs of spawning adults (odd years 1957–67). By 1979, a population explosion occurred in Lake Superior and the species completed expansion of its range into all the Great Lakes. Interestingly, this species became the only naturally self-sustaining introduced species in the Great Lakes, despite assumptions that it was an obligatory anadromous species, requiring a seawater environment to reach sexual maturity (Rounsefell 1958).

In the event that an ecologically noxious type of transgenic fish were to disperse and persist over a large area, controlling its abundance would not be easy and could be impossible. Chemical controls, such as that used for lamprey control in the Great Lakes, are costly and may not be specific enough in their impact to avoid damaging other species in the community. Effective biological controls are often difficult to identify and implement. Physical controls, such as application of certain harvesting strategies or modification of habitats, are generally expensive and often ineffective.

Scale and Frequency of Introduction

The scale and frequency of introductions of transgenic fish into a particular environment will greatly influence the degree of ecological risk involved. A critical mass of introduced individuals may be needed for some of them to survive the numerous forces of natural mortality. Although surprising outcomes cannot be ruled out *a priori*, low ecological risk may be a reasonable conclusion in situations where phenotypic and ecological attributes of transgenic individuals raise concerns, but the scale and frequency of their introduction are so small that their chances of becoming established in the natural setting are extremely low.

Frequencies of introductions must be considered in terms of seasons and longer time periods. Seasonal timing will influence the success of an introduction due to related timing of food availability, predator concentration, and other factors influencing fitness of introduced individuals. Due to interannual variation in quality of these seasonal factors, introductions, particularly small-scale ones, may have to be repeated over a number of years before transgenic individuals will become established.

Finally, planned rather than accidental introductions are much more likely to lead to persistence of transgenic fish in the environment, unless the scale or frequency of an accidental introduction is sufficiently great to overwhelm other obstacles. This can be great; for example, we recently presented concerns about culturing ecologically risky transgenic fish in commercial net-pen operations because of existing evidence that significant numbers of farmed fish regularly escape net pens and persist in the surrounding natural environment (Hallerman and Kapuscinski 1992).

Implications for Fisheries Management

Fisheries managers will experience several repercussions if ecologically noxious transgenic fishes becomed established in aquatic ecosystems. These fish could destabilize and reorganize the recipient ecosystem (reviewed by Kapuscinski and Hallerman 1990). Such consequences will reduce abilities of managers to forecast future behavior of the entire system. Estimation of sustainable yields and responses of the resource to a suite of management actions will become more difficult.

Planned introductions of transgenic fish to enhance exploited populations are likely to dramatically increase user expectations of miraculous improvements in the fishery. Thus, complex political pressures on resource managers will increase (Chase 1987; Gale 1987). This could even further limit currently difficult efforts to base resource management on ecologically sound principles. For example, planned releases of transgenic fish bearing extra growth hormone genes would create expectations that these fish will reach large sizes in a relatively short time. Increased interest in the fishery might motivate politically powerful users to influence managers to permit greater fishing pressure. Predictable declines in abundance of less productive stocks (in the case of a mixed stock fishery) and other interacting species known to be important for the health of the entire aquatic community would then be ignored. Ironically, these declines could eventually indirectly depress the growth and survival of the stocked transgenic fish.

Efforts to conserve natural genetic diversity of fisheries resources may also suffer from establishment of some transgenic fishes in aquatic ecosystems. Transgenic fish whose phenotypes are ecologically analogous to noxious introduced species might reduce species diversity quite directly through any altered competitive or predator-prey interactions with other organisms. Introduced species, representing novel phenotypes in an ecosystem, contributed to 68% of the extinctions of North American fish species during the past century (Miller et al.

1989) and have been implicated in the disappearance or decline of species in waters of other continents (Welcomme 1988).

Introgressed transgenes derived from fertile transgenic individuals will modify the genetic makeup of natural populations. Evolutionary consequences for natural fish populations are unclear and should be considered by biologists. Introgression of transgenes would also confound future surveys of natural patterns of genetic variation within and between species. Such surveys will be of increasing importance to fisheries managers who will need data on which to base difficult choices about population structures and distribution as they seek to protect genetic diversity from the current trend of mass extinctions.

Conclusion

Much uncertainty surrounds the ecological implications of introducing transgenic fishes into natural ecosystems. While some transgenic fish should prove to be ecologically innocuous, transgenic fishes as a group have the potential for significant impact because of the fitness of most fish stocks in natural settings (Tiedje et al. 1989; Kapuscinski and Hallerman 1990). Research aimed at producing economically important transgenic fish is advancing rapidly. Thus, ecologically sound approaches to reducing existing uncertainties must be implemented in a timely fashion.

A disturbing fraction of ecological tragedies have been the result of administrative misjudgement (Laycock 1966). Recently, we have seen the devastating effects of the planned introduction of nile perch (*Lates niloticus*) into Lake Victoria. While some decision makers considered this introduction a success because it led to significant increases in commercial catches, it had tragic consequences for species diversity. This introduction is probably responsible for the extinction of over 300 endemic species of haplochromine cichlids (Welcomme 1988; Ogutu-Ohwayo and Hecky 1991). Professionalism demands better in the future.

Performance evaluations of transgenic fish are solely needed to gain insight into their potential ecological impacts. Two complementary approaches are needed: a battery of laboratory experiments, where a few environmental factors are varied while others are held constant; and studies in more ecologically realistic but securely confined mesocosms (Odum 1984; Voshell 1989). Interdisciplinary teams of aquatic scientists versed in ecology, population dynamics, physiology, behavior, ichthyology, genetics, evolutionary biology, risk assessment, and resource management and conservation must be assembled to develop protocols for risk assessment, containment, and confinement of transgenic fishes and to identify related research needs. Such protocols should be based on accumulating performance data and must be general enough to accommodate other transgenic aquatic animals and plants that may be developed in the future.

One possible aid in risk management is to determine if the expressed phenotypes of transgenic fish are similar to phenotypes of species that have existed for long periods of time in a particular aquatic ecosystem with no negative ecological consequences. This idea of evaluating familiarity of transgenic organisms has been suggested for microorganisms (National Research Council 1989, p. 127). Fisheries scientists need to carefully evaluate its merits and limitations for risk evaluations of transgenic fishes.

Given the current situation of uncertainty, intentional stocking of transgenic fishes in natural waters should be opposed and their use in production-scale aquaculture should be restricted. These recommendations were promulgated by the American Fisheries Society in a recent position statement on transgenic fishes (Kapuscinski and Hallerman 1990a).

No research and risk assessment program, no matter how comprehensive in scope, will cover all possible outcomes of introducing transgenic fishes into natural ecosystems. If conservation of natural aquatic ecosystems is to have a chance, we must invoke humility rather than *hubris* in predicting ecological impacts, and in promising safe uses of transgenic fishes.

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Aquaculture and Hatchery Implications

Introductions as Factors in Diseases of Fish and Aquatic Invertebrates[1]

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Fish and invertebrates are subject to a wide range of disease agents. Many of their diseases are probably local in origin although a lengthy list of infections were probably imported via the vast array of exotic species which have been transferred to virtually all areas of the world. Since all living organisms carry a full suite of microorganisms and larger parasites the likelihood of there being pathogens for local species among them is good. Introductions can occur in at least one of three separate ways: (1) intentional introductions for specific purposes, (2) accidental transport of biological agents via massive transfers of ballast waters or (3) through the ornamental or aquatic pet trade. Control measures and information services devised by the International Council for the Exploration of the Sea, the European Inland Fisheries Advisory Commission and the Office International des Epizooties are described.

Les poissons et les invertébrés sont sujets à de très nombreux agents pathogènes. Bien des maladies sont probablement d'origine locale, bien que de très nombreuses autres infections aient probablement été importées avec les espèces exotiques introduites dans pratiquement toutes les parties du monde. Étant donné que tous les organismes vivants transportent une faune de micro-organismes et de parasites plus grands, la probabilité qu'ils transportent des pathogènes pour les espèces locales est très grande. Les introductions peuvent être faites de trois façons : (1) intentionnellement, dans un but précis, (2) accidentellement, par transport d'agents biologiques avec l'eau utilisée comme lest, (3) par l'intermédiaire des animaux aquatiques importés pour les aquariums. On décrit les mesures et les services d'information conçus par le Conseil international pour l'exploration de la mer, la Commission européenne consultative pour les pêches dans les eaux intérieures et l'Office international des épizooties.

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Disease has been defined by Kinne (1984a) as a "demonstrable negative deviation from the normal state (health) of a living organism." In this definition negative deviation "implies an impairment quantifiable in terms of a reduction in the ecological potential (eg. survival, growth, reproduction, energy procurement, stress, endurance). The deviation may be functional or structural or both; it may result from a single cause or from several causes acting in concert." Thus the term disease as used here has an ecological perspective since a disease as well as affecting the individual and its populations can also affect functionally related species, i.e., prey, predators, and competitors. The resulting modifications to distribution and abundance of the organisms will affect the patterns of flow of energy and matter. As a consequence of this Kinne has insisted that the study of diseases of marine organisms should be central to marine as well as other aquatic ecological research. He contends that since the majority of studies on organism performance under environmental change have been conducted without due consideration for disease, adequacy of nutritional and environmental conditions or appropriate acclimation they can only be crude assessments at best of the metabolism of individuals or their mortality rates. Further, they are unlikely to be adequate for gauging population or species specific potentials for reproduction and competition or long-term adjustment to ambient stress at the population level.

Fish and aquatic invertebrates, in keeping with all living organisms, are subject to disease. A partial list of diseases observed for species under culture in countries belonging to the International Council for the Exploration of the Sea (ICES) (Table 1; Stewart 1991) illustrates the diversity of infections which range from relatively mild interferences with health and well-being to those causing mass mortalities. The diseases of finfish are the best studied of all those affecting aquatic species, but even here only a small fraction have been investigated well; Kinne (1984b) estimates that less than 2% of the fish diseases are known and even for these the knowledge is incomplete. Comprehensive accounts of the wide spectrum of diseases affecting aquatic species can be found in such works as the series edited by Kinne (1980 et seq.), Sindermann and Lightner (1988), Roberts (1989), and Sindermann (1990).

Many of the studies of diseases of aquatic species have been conducted on animals held in captivity in hatchery and/or grow-out operations, in experimental and commercial culture. With the production of immense tonnages through culture (approximately 12 000 000 t in 1986 equal to 12% by weight and more by value of the total commercial production) of finfish, molluscs, crustaceans and seaweeds (FAO 1989) the scales of disease outbreaks locally and commercially become correspondingly large. With this increasing production the impetus for studies on the diseases to which these species are susceptible

[1]This paper forms part of the Proceedings of the Ecological and Genetic Implications of Fish Introductions Symposium (FIN) convened at the Great Lakes Institute, University of Windsor, Ontario, Canada, May 17–19, 1990.

TABLE 1. Representative diseases and pathogens of marine and anadromous species in ICES countries.

Agent or sign	Host species	General location	Time of year
Vibrio anguillarum	Atlantic salmon Rainbow trout, cod, halibut, Charr, Turbot.	N. Europe	summer & fall
V. ordali	Rainbow trout, salmon.	W. Atlantic	summer & fall
V. salmonicida (Cold water disease)	Atlantic salmon, Rainbow trout	N. Europe	year round
Bacterial Kidney Disease *Renibacterium salmoninarum*	Atlantic salmon Rainbow trout	Atlantic and Pacific	year round
Furunculosis *Aeromonas salmonicida*	Atlantic salmon, Oncorhynchus	Atlantic and Pacific	sumer and fall
Enteric Redmouth (*Yersinia ruckerii*)	Rainbow trout	Atlantic and Pacific	summer to fall
Pancreas disease unknown agent	*Atlantic salmon*	Atlantic	spring to fall
Mycobacteriosis	*Atlantic salmon*	Atlantic	winter
Sea Lice	*Atlantic salmon*	Atlantic	year round
Infectious Pancreatic Necrosis (IPN) Virus	*salmonids*	Atlantic and Pacific	swim-up
Ichthyophonus	*Pleuronectes platessa*, haddock, herring	Atlantic	
Pseudobranch swelling	Cod	Atlantic	
Skin ulcer Hyperplasia papilloma	*Limanda limanda*	Atlantic	
Lymphocystis	*Limanda limanda*	Atlantic	
Cadhemia (*Aerococcus viridans*)	Lobster (*Homarus*)	Atlantic	summer and fall
Bonamia ostreae	*Ostrea edulis*	Europe	year round
Minchinia	*Crassostrea virginica*	Atlantic	year round
Perkinsus sp.	*Venerupis*	Atlantic	spring
Marteila	*Mytilus edulis*	Atlantic	year round
Protozoan (Denman Island)	*C. gigas*	N. Pacific	
Fatal Inflammatory Bacteremia	*C. gigas*	N. Pacific	Jan.–Oct.
Larger parasites	All species of finfish and shellfish	Atlantic and Pacific	

In addition, great resulting in a significant increase in fish disease information. Diseases in the wild species have received attention usually only when mass mortalities have occurred and the populations which have been materially affected and thereby drawn attention.

All organisms carry, as a normal complement, a full suite of organisms from among the viruses, rickettsia, bacteria, yeasts, fungi and larger parasites, the composition of which is usually unique to each species. Some of these are opportunistic pathogens for the species carrying them, i.e., they become effective in causing disease if and when the health and defense mechanisms of the host are impaired by factors such as nutritional deficiencies, adverse environmental conditions, excessive densities etc.; the agent can then flourish causing an overt infection and may be just as effective in causing mortalities as the highly specific pathogens. Others within this suite may cause the host species little or no harm regardless of circumstance, but may be highly pathogenic for other species with which the host may come in contact. Thus, other plants and animals frequently are carriers, reservoirs or vectors of disease within a region.

The eel parasites *Anguillicola crassus* and *A. novaezelandiae* are believed to have been introduced to Europe with live eels (*Anguilla* sp.) from the Far East or New Zealand in the early 1980's (Peters and Harmann 1986 and Taraschewski et al. 1987). They are well established in Europe where up to 70–90% infestation rates are now common among local eels, *Anguilla anguilla*, (Peters and Hartmann 1986; Hartmann 1989). These nematodes live as parasites in the swim bladders of eels where they suck blood from the swim bladder walls. The eels first become infested at 20 cm; the infestation increases up to an eel length of 40 cm. A heavy infestation reduces the hardiness of the eels in captivity making them difficult to transport and market. Because the parasites are firmly established in European fresh waters and the supply of eels for culture must be obtained from wild populations, the parasites are a major economic threat (Peters and Hartmann 1986). This is an excellent example of the spread through commercial trade of a dis-

ease agent which is more pathogenic for a local species than it is to the original host.

One striking example of an entirely new disease being created, it is believed, is the fungal disease "krebspest" first noted in 1860 in Italy (Unestam 1973). This disease caused by the fungus, *Aphanomyces astaci*, has, since 1860, gradually eliminated the highly valued crayfish, *Astacus astacus* from most of Europe. Although impossible to prove now, the fungus is believed to have been transferred to the susceptible European crayfish by the introduction of *Pacifastacus* from America, species of which carry the *Aphanomyces astaci* as part of their normal microflora. The fungus does not cause a disease in the American crayfish; the European crayfish, however, is completely susceptible and infections are invariably fatal. The spread of the fungus has eliminated an important fishery, food item and a vital member of the ecological community from virtually all of continental Europe.

One of the most important and destructive salmonid diseases is furunculosis caused by the bacterium, *Aeromonas salmonicida* (see Table 1). It appears to be endemic to virtually all salmonid areas, on occasion causing large losses in hatcheries and massive mortalities among both wild and cultured salmonids. It was first described in brown trout in hatcheries in Germany and subsequently in natural trout rivers in Germany and other countries in central and western Europe (Margolis 1954). From there, it was suggested by some in the 1950's, it could have been transported to Britain via infected brown trout transfers and ultimately to the United States in the early part of the twentieth century. A counter suggestion has been made by R. J. Roberts (pers. comm.) that *A. salmonicida* is almost certainly a pathogen of rainbow trout and Pacific salmon and thus was probably introduced originally to Germany from North America. There is no question, however, about a more recent transfer. Atlantic salmon smolts imported to Norway from Scotland to supplement supplies available to farmers gave rise to many farm outbreaks caused by a biotype of *A. salmonicida* more virulent than any previously detected in Norway (Munro 1988). As a result, the stock of more than 20 Norwegian sea farms was slaughtered in an attempt to eradicate the disease; the total damages were estimated to exceed 100 million US dollars. Since it is now almost ubiquitous in salmonid areas furunculosis along with Bacterial Kidney Disease and sea lice is a major economic threat to salmon farmers; especially those rearing Atlantic salmon (*Salmo salar*) where world production is now approaching 300 000 t/yr valued at around $2,000,000,000.

The difficulties inherent in determining whether a pathogen has been introduced into a new geographic area is illustrated by events surrounding the initial detection of viral hemorrhagic septicemia virus (VHSV) in North America. This virus causes annual losses equal to 40 million U.S. dollars among farmed rainbow trout in Europe and legislation in the United States and Canada requires the emergency destruction of fish found to be infected. In the fall of 1988, VHSV was detected in normal adult chinook and coho salmon returning to hatcheries at two locations near Puget Sound in Washington State. This initial isolation of VHSV necessitated the destruction of approximately four million fish at the affected hatcheries (American Fisheries Society, Fish Health Section Newsletter 17:2:1–4, 1989). Because VHSV was regarded as unique to Europe, it was widely believed that the virus had been imported and efforts were mounted to determine the extent to which the virus had become esablished in North America. Surveys for VHSV among 20 000 fish collected in neighbouring British Columbia failed to reveal its presence (G. E. Hoskins, pers. comm.) and expanded surveys of marine and freshwater fishes in the states of Washington and Oregon did not produce additional isolates. In the fall of 1989, VHSV was isolated from normal adult coho salmon at two different locations close to seawater in Washington State; however, fish at hatcheries affected the previous year were negative. While initial examination of the North American isolates of VHSV showed them to be serologically indistinguishable from European strains of the virus, further research showed the Washington isolates had greatly reduced virulence for rainbow trout and were somewhat different at the genetic level (J. R. Winton, pers. comm.). The close association of the North American isolates with the marine environment, their lower pathogenicity, and their genetic differences suggested these strains are different from the typical European trout strains and may not have been imported. In the summer of 1990, VHSV was isolated from a Pacific cod in Prince William Sound, Alaska. This new isolate, coupled with a report from Europe that VHSV had been isolated from Atlantic cod in Denmark, gave rise to a new, but highly tentative, working hypothesis. This theory proposed that VHSV is principally a virus of one or more species of marine fish in both the Atlantic and Pacific oceans and that anadromous fish in North America may have become infected by recent contact with marine fish. In Europe, the virus may have been introduced into rainbow trout facilities by using unpasteurized marine fish products as food. The continuous presence of the virus in European trout culture presumably would allow adaptation to and an increase in virulence for trout. Much additional work is needed, however, before our understanding of the epizootiology of VHSV is adequate (J. R. Winton, pers. comm.).

One of the best documented examples of a disease spread through introductions is bonamiasis, the disease of the flat oyster, *Ostrea edulis*, caused by the protozoan parasite, *Bonamia ostreae*. Apparently, it is transmitted readily and directly (oyster to oyster) and within 6 months of its introduction to dense but uninfected populations, it caused mortalities of up to 80% (Balouet et al. 1983 and Elston et al. 1986). Stress seems to be an important factor in lowering resistance to the parasite and is probably the main reason why cultured flat oysters suffer greater mortalities than do the natural stocks, which are left virtually unhandled throughout their growth cycle. According to Elston et al. (1986) infected *O. edulis* spat from Elkhorn Slough, California was the source for the spread of the disease to other parts of North America and its introduction to Europe; unfortunately, these authors were unable to reconstruct its earlier history. The disease, in Europe, was first recognized in Brittany in 1979 (Comps et al. 1980). It was introduced to the Netherlands in 1980 in lots of oysters imported from France, specifically to the Yerseke Bank oyster area (Van Banning 1991). By 1988, the Yerseke Bank commercial production of the flat oyster had been eliminated as a result of the parasitization and the other *O. edulis* production area, the confined salt water lake, Lake Grevelingen, had been invaded by the parasite, presumably via the hulls of boats passing from Yerseke Bank to the Grevelingen. Similar importations from Brittany transferred infected flat oyster seed to estuaries in Galicia, Spain and established the parasite there with comparable results (Montes et al. 1991 and Figueras 1991). In Ireland, it is generally believed that an illegal consignment of oysters from France introduced the parasite to the southwest of the country in the early 1980's from whence it was spread to other oyster-producing areas (McArdle et al. 1991). The observations made in the United

Kingdom trace the present distribution, of the parasite, in Engand to one event in Fal, Cornwall (its presence in England was first confirmed there in 1982) where, it is suggested, introductions from continental Europe had taken place; since then, it has spread widely in southern England where its presence has been confirmed in seven separate locations (Hudson and Hill 1991). The economic consequences of bonamiasis for the flat oyster industries in all of the countries listed has been extremely serious. Countermeasures are being devised in attempt to minimize the impact on the cultivation of the flat oyster and to halt its spread to any uninfected natural stocks.

Not all threats to the well-being of fish and invertebrates come necessarily from direct infections. Blooms of various phytoplankton have also had serious negative effects on aquatic populations. One such example, which fits the ecological perspective of Kinne's disease definition, is the dinoflagellate, *Gyrodinium* cf. *aureolum* (Mahoney et al. 1990) believed to have been introduced relatively recently to North America. Probably transported from Europe it was first seen in the Carmans River, New York in 1982 and again in 1983. Subsequently it was found in large concentrations along the coast of New Jersey between Cape May and Sandy Hook in 1984 and 1985 and again in Maquoit Bay, Maine in 1987. Kills of blue mussels, *Mytilus edulis* and lady crabs, *Ovalipes ocellatus* were observed coincident with a bloom off the New Jersey coast; sport fishermen reported reduced catches and assumed that the fish were avoiding the area because of the *Gyrodinium* concentrations. People reported nausea, sore throat, eye irritation and lung congestion after exposure to bloom waters. These authors state that although the effects of this bloom were not critical in New Jersey, the presence of the species should be regarded as having great potential for harm to marine life; since its first detection in Europe in 1966 it has become the most important and notorious dinoflagellate in the North Sea and in the coastal waters of Ireland, England, Denmark, Norway and Sweden. There, it is associated with extensive mortalities occurring among a considerable number of marine fish and invertebrate species; biotoxins produced by the *Gyrodinium* may have been involved in many of the kills.

These examples serve to make clear several points concerning diseases and their introduction to new areas. The first is that although many diseases are suspected to have been introduced in one manner or another, irrefutable evidence is usually lacking. The disease in question is observed usually long after the time of the putative introduction and the connection can be made by deduction or inference only. It may be that the disease did occur locally, but went undetected or unrecognized because of lack of interest, knowledge, or qualified investigators. Secondly, diseases are at least as common and can be as destructive to aquatic species as to terrestrial forms, resulting in mass mortalities, jeopardizing economic enterprises, whole populations and sometimes resulting in the extinction of entire species. This aspect alone should warrant strenuous efforts to study and understand the various diseases and devise sound countermeasures. Thirdly, not only are the aquatic species subject to the diseases of the area in which they live, but with the widespread transfer of various species the hazards have been increased by exposing local species to exotic microorganisms and larger parasites. Aquatic species, molluscan shellfish in particular, are noted for their capacity to concentrate, without harm to themselves, viruses of all kinds; these viral and other microbial collections could include known pathogens of aquatic species, and novel forms which could cause disease among

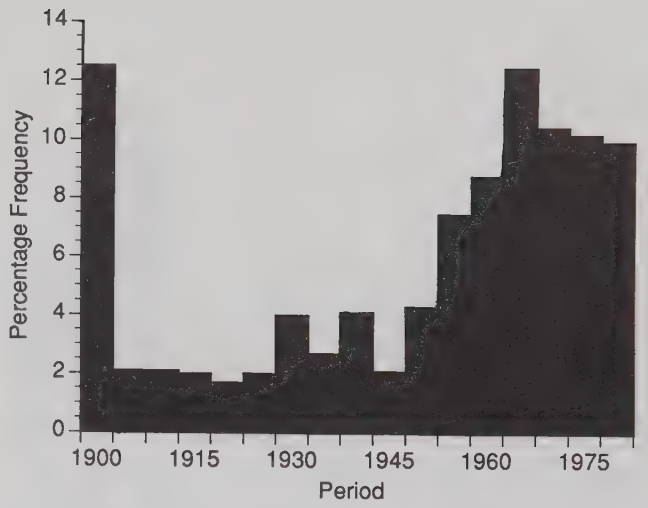

FIG. 1. Percentage of total transfers, since 1900, of exotic freshwater and anadromous species by 5-yr intervals. (Redrawn from Welcomme 1986.)

naive communities. Finally, the phytoplankton both resident and possibly introduced are becoming increasing hazards to wild and cultured stocks. Problems are caused through production of biotoxins, physical impact of the dense growths or by mass die-offs which reduce oxygen values in bays and inlets through decomposition of the algal biomass.

Two questions immediately arise: (1) How are diseases transferred and introduced to new areas? and (2) What if anything can be done to reduce or eliminate the transfer of diseases?

The answer to the first question is that the pathogens themselves are concomitants, with unfortunate consequences, of transfers made wittingly and unwittingly as illustrated previously. There are at least three activities which result in the transfer of species, with their accompanying burdens of specific and potential infective agents. These are:

1) Formal or recorded introductions of species.
2) Accidental introductions through transfers of ballast waters.
3) Trade in ornamental and aquatic pet species.

Welcomme (1986), on behalf of the United Nations Food and Agricultural Organization (FAO), documented the transfers from the waters of one country to those of another between 1900 and 1985. These data (Fig. 1, 2, and 3) show clearly the large scale of transfers and introductions in this century alone. Since these data were published, FAO has continued to expand its collection of information; the latest update (R. L. Welcomme, pers. comm.) shows that the register for international introduction of inland water species now has a total of 1,673 introductions of 291 species into 148 countries dating back to the middle of the nineteenth century. Welcomme (1986) speculated that a decline in the rate over the past couple of decades might be the result of a saturation effect in which most candidate species would already have been transferred to the majority of receiving countries. Welcomme (1986) in his review divided the major introductions into three waves. The first consisted of the salmonid introductions of the 19th century and the early part of the 20th century. This was followed by transfers of tilapine cichlids mainly from 1950 to 1970 and thirdly the recent movements of the Chinese carps. Other species were being introduced concurrently with emphasis on mosquito-eating fish in the 1930's and 1940's, and today on new species for aqua-

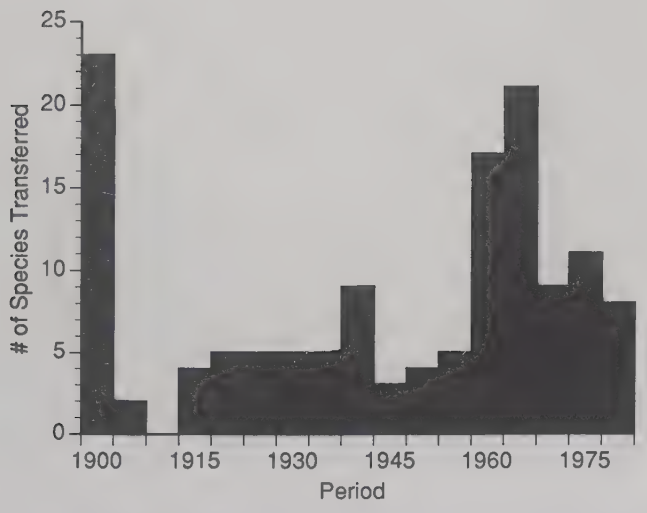

FIG. 2. Number of freshwater and anadromous fish species involved in transfers where first date of transfer is known. (Redrawn from Welcomme 1986.)

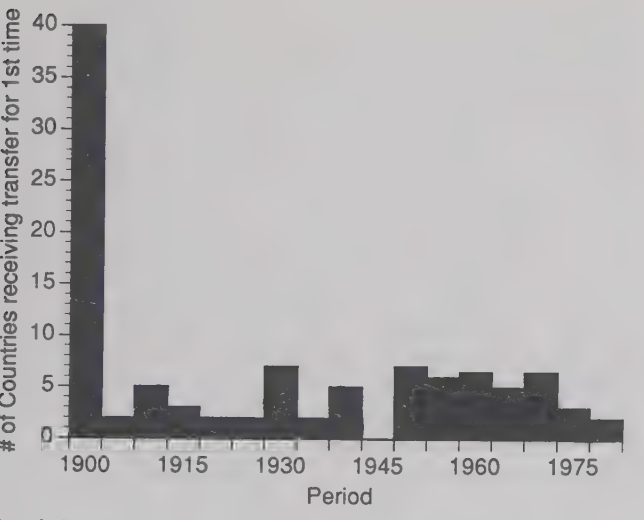

FIG. 3. Number of countries receiving introductions of freshwater and anadromous fish species where first date of transfer is known. (Redrawn from Welcomme 1986.)

culture. The objectives of these transfers included the improvement of recreational fishing and productivity of natural water bodies, control of undesirable aquatic organisms, ornamental species and aquaculture. These data include only freshwater and anadromous species with most of the transfers taking place before there was any significant knowledge of fish diseases and hence virtually no precautions were applied to prevent the simultaneous transfer of noxious agents.

Similarly as Sindermann (1986) has pointed out, one important consequence of the global expansion of marine aquaculture (mariculture) has been the large scale movement of plants and animals to areas where they have not previously existed. With the continuity of oceans and lack of barriers the opportunities for the continued spread of the introduced species to new areas is excellent and with this comes the risk of disease.

The transfer of freshwater species through the intentional introductions reported by Welcomme (1986) and for the marine aquaculture industry referred to by Sindermann (1986) are complemented if not dwarfed by the massive ballast water biological transport system operating over vast distances. The resultant biological invasions have been described in detail by Carlton (1985 and 1989). "Ballast water transport is the movement of living organisms in the water of ballast tanks of vessels. Such movement can be along coasts, into inland waterways and lakes, along and through canals, and across and between oceans. The waters may be fresh, brackish or marine. The organisms are those species in the water column. These include nekton, holoplankton, meroplankton, demersal zooplankton, and tychoplankton, i.e. benthic species which are passively swept up into overlying waters by water turbulence, such as wave action and tidal currents or by the action of a vessel's propellers" (Carlton 1985). The use of ballast water dates from the 1850s and became significant by the 1880's. It was used to replace solid ballast material to reduce the time and expense of loading and unloading dry ballast materials. The individual capacity of the thousands of vessels with water ballast tanks ranges from hundreds to hundreds of thousands of gallons. The water may be pumped aboard or the tanks filled by gravity. The amount loaded and the period for which it is carried will be matched to cargo, route, destination, fuel loads and weather conditions. Thus water may be taken on at the beginning of the voyage and added to en route. The discharge can begin prior to reaching the destination and occur in port or inland waters. Patterns of ballast water movement over the past 100 years have paralleled the world's shipping routes which have altered materially with time. There are now approximately 40 000 major ships in which billions of tonnes of ballast waters are carried annually on at least one leg of each trip. With the vastly greater quantities of water carried at greater speeds (thereby shortening the holding times and hence stress on captive life forms) the opportunities for successful transfer of organisms are increased. All of this is additional to the transport of fouling organisms attached to the exterior of the ships. The prospects for aquatic living forms being transferred from all parts of the globe to any other point have improved significantly over recent years. One representative example of several cited by Carlton (1985) serves to illustrate this. Investigators commissioned by the Canadian Environmental Protection Service sampled the ballast water of 55 merchant vessels from many countries in the summer and fall of 1980 as the vessels entered the Great Lakes through the St. Lawrence Seaway at Montreal. Identifiable living organisms were found in 51 of the 55 vessels examined.

Carlton (1989) concluded that extensive local alterations of the natural diversity and of natural distribution of many species has occurred over the past 100 years as a result of the discharge of water ballast. He estimates conservatively that well over a thousand marine species have been translocated plus a significant number of freshwater taxa. He goes on to cite and document in habitats as diverse as coastal dunes, estuaries, rocky shores and coral reefs that introduced species now predominate in various parts of the world. Carlton (1985) gives lengthy lists of species, ranging from the phylum Cnidaria to the phylum Chordata, as introduced from and to all of the different continental areas. In one particularly interesting example Carlton (1989) enumerated, for the South Slough National Estuarine Research Reserve, Coos Bay, Oregon, the introduced species, along with their origins and mechanisms of introduction. This list includes a number of species in each category and is composed of Porifera, Coelenterata, Annelida, Mollusca, Crustacea, Bryozoa, two teleost fish species (American Shad and Striped Bass), Phaeophyta (*Sargassum muticum*) and Angiosperma (*Zostera japonica*). The fish, Phaeophyta and Angio-

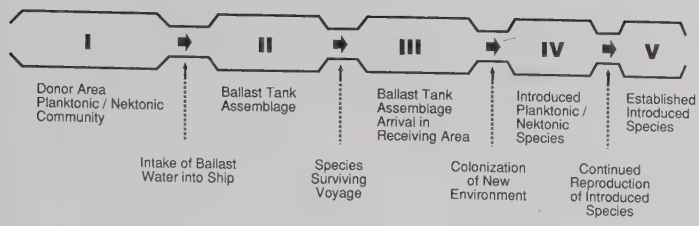

FIG. 4. Sequence of events in the dispersal and introduction of exotic species in ship's ballast water emphasizing various steps and choke points. (Redrawn from Carlton 1985.)

sperma were attributed solely to deliberate plantings; the rest were attributed to a mixture of introductions as fouling organisms on the hulls of vessels, ballast water organisms, and as incidental passengers on transfers in the commercial oyster industry and others. About half had an involvement with ships. a second example is the very well-documented establishment and proliferation of the Asian clam, *Potamocorbula amurensis*, in San Francisco Bay (Carlton et al. 1990). Although not recorded there prior to 1986, it has since become very abundant (in some cases reaching densities of 10 000 m^2) giving rise to fears that it might result in major alterations to the Bay ecosystem by causing changes in both trophic and benthic dynamics. Thus, not only does this event introduce a new suite of coincident organisms and the risk of transferring diseases, but by also changing the relationships among species so dramatically it provides a markedly enhanced opportunity for development of entirely new diseases. A scenario, consistent with both examples, can be developed for many parts of the world in both marine and freshwater areas. Carlton (1985) has pictured the overall transfer process in a model which has been redrawn and shown as Fig. 4.

The third important source of transfers and introductions is the largely unregulated trade in ornamental species and aquatic pets. The problem arises not only from species imported for immediate sale or for establishng breeding colonies, but also from the disposal of the water in which these species were transported. Since much of the trade consists of moving tropical species to colder temperate zones, the belief is that the likelihood of these species surviving locally is not great. As everyone will recognize, however, the establishment of even one, e.g. the Walking Catfish, can cause major problems. Apart from this, the uncontrolled disposal of millions of gallons of transport waters in which the organisms are shipped without regard for contaminating or incidental organisms which this water might contain increases the hazard of introducing pests and pathogens of all sorts into the new environment.

One aspect which is not always considered sufficiently in discussions of introductions is the fact that capacities or properties can be transferred successfully to a new location through movement of the genetic material alone. Studies such as those by Paul et al. (1987) have shown that deoxyribonucleic acid (DNA) is released continuously from bacterioplankton through death and lysis, grazing by bacteriovores and excretion. Their work in estuarine and oceanic environments showed that the DNA can persist for lengthy periods; the turnover time ranged from a low of 6.5 h in a eutrophic estuary to periods ranging between 32 and 90 days in other marine areas. The persistence of intact genetic material in the environment provides the mechanism for transfer of new traits including disease capacities to previously innocuous local organisms without the immediate presence of the intact deleterious agent. Opportunities for transfers via genetic material alone should be of prime concern when considering the hazards inherent in ballast water releases and in disposal of waters used to transfer species for introduction or in the aquatic pet trade.

The second question posed was: What can be done to reduce or eliminate the transfer of disease? Some steps have been taken already. In 1973 (Turner 1988), ICES adopted a "Code of Practice to Reduce the Risks of Adverse Effects Arising from Introductions of Non-indigenous Marine Species"; this was revised in 1979 and amplified in Turner (1988). A comparable and cooperative activity was carried out by the FAO organization, the European Inland Fisheries Advisory Commission (EIFAC); a description of the required procedures in the Codes of Practice endorsed by both organizations is contained in Turner (1988). The approach in the "ICES Code of Practice" to be used for introductions has been summarized by Sindermann (1986) in the form of 6 steps which, if taken, will reduce the likelihood of disease transfer when introducing non-indigenous species to either marine or freshwater areas:

1) Conduct comprehensive disease studies in the native habitat of the species proposed for introduction.
2) Transfer individuals of the species to a closed system in the receiving area where they are to be maintained, studied, and examined for disease.
3) Select healthy individuals for development of a brood stock for this species from within this closed system.
4) Grow the F_1 individuals in isolation from the brood stock and destroy the original brood stock.
5) Make small-scale introductions of healthy F_1 individuals into the natural waters of the recipient area and continue disease studies on these individuals.
6) If no signs of disease occur, use these F_1 individuals, to build a local brood stock and thus eliminate the need for further transfers of this species.

In addition to the ICES/EIFAC approach described above, which all member nations have endorsed and it is expected will be putting into practice, there is another initiative which should also be beneficial. The Office International des Epizooties (OIE), established in 1974, and headquartered in Paris is an international veterinary organization representing 110 countries. Its main objective is to promote awareness of diseases associated with trade in live animals and the means for their control and prevention (de Kinkelin et al. 1990). There are two categories of listed diseases; List A comprises 16 communicable diseases which have potential for rapid spread and serious socio-economic or public health consequences and are of major importance in the international trade of animals and animal products. List B comprises 89 communicable diseases with similar attributes, but of lesser importance to humans than those in List A; pathogens contained in List B are, however, of major consequence to fish and shellfish. The OIE deals with fish diseases through its Fish Disease Commission (FDC) which produces an annual report on current diseases and new pathogens as well as on diagnostic and control methods. The section on fish diseases is being revised and will contain in List B those pathogens of fish (including shellfish) depicted in Table 2. The OIE through its activities and Bulletin provides a global network for rapidly disseminating news of diseases in aquaculture. The complaint is made, however, that although this comprehensive international system exists "it is badly under-utilized for aquaculture situations" (de Kinkelin et al. 1990).

The problems associated with the biological transfers and invasions arising from ballast water discharges are even more

TABLE 2. Office international des epizooties/Fish Diseases Commission. Animal Health Code (LIST B Pathogens for Fish).

Fish	Shellfish
Viral haemorrhagic septicaemia virus (VHSV)	Molluscan pathogens
Infectious haematopoietic necrosis virus (IHNV)	*Bonamia ostreae*
Spring viraemia of carp virus (SVCV)	*Bonamia* spp.
Herpesvirus of salmonids type 2 (OMV)	*Haplosporidium nelsoni*
Herpesvirus of ictalurids type 1 (CCV)	*Marteilia refringens*
Enzootic haematopoietic necrosis virus (EHNV)	*Marteilia sydneyii*
Renibacterium salmoninarum	*Perkinsus marinus*
Edwardsiella ictaluri	Iridoviruses
	Crustacean pathogens
	Infectious hypodermal and haematopoietic necrosis virus (IHHNV)
	Monodon baculovirus (MBV)
	Baculovirus penae (BP)
	Midgut gland necrosis virus (BMN)

difficult. It has been argued that no precautionary steps need be taken since everything of potential harm has probably already been transferred. This argument fails to recognize that shipping patterns and routes have changed, ships have become larger and faster and feature more transequatorial and longer trips than ever before. Because of a lack of qualified observers, detection of events such as troublesome introductions of phytoplankton and animals (e.g. zebra mussels) may occur only when the problem becomes acute. One measure, devised by the Canadian Coast Guard at the urging of the Great Lakes Fishery Commission as a voluntary interim guideline, was to exchange ballast water already on board with high salinity water on the high seas. The exchange, it is believed, would reduce the risk of introducing freshwater species to areas suitable for their propagation (Kerr, 1990). The use, as ballast, of fresh water matching municipal drinking water standards, although costly, would probably completely eliminate the problem for both marine and fresh water areas.

If transfers and introductions, and the consequent diseases and pests are to be controlled it will be necessary to:

1) Institute inspection and certification programs.
2) Provide supporting research facilities.
3) Negotiate through appropriate bodies sound international codes and protocols such as those devised by ICES and EIFAC.
4) Devise appropriate national regulations.

In this context, an interesting start has been made by the European community in considering draft regulations based on health status to control movement of aquaculture animals and products by member countries, thereby reducing the spread of disease (Munro 1991).

Examination of the problems created by transfers and introductions of non-indigenous species is somewhat discouraging in view of the massive scale of the three activities examined here. It is, however, worthwhile to remember and repeat the response given by Dr. C. J. Sindermann, a staunch advocate of controls, in answer to pessimistic views expressed about the prospect of making headway against the apparently worldwide and determined efforts to transfer all species from their present locality to everywhere else. "If the goal is worthwhile, one must always persist no matter what the nature of the problem, if nothing else, one must provide an oasis of sanity in an otherwise irrational world because somewhere someone might be paying attention."

Acknowledgements

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Are Cultured Stocks of Brown Trout (*Salmo trutta*) and Rainbow Trout (*Oncorhynchus mykiss*) Genetically Similar to Their Source Populations?[1]

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Ferguson, M. M., P. E. Ihssen, and J. D. Hynes. 1991. Are cultured stocks of brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) genetically similar to their source populations? Can. J. Fish. Aquat. Sci. 48 (Suppl. 1): 118–123.

The Ontario Ministry of Natural Resources (OMNR) implemented a controlled breeding program in the early 1980's with the objective of culturing fish that are genetically representative of the source populations. We describe the OMNR brookstock management plan for brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) and test its effectiveness by comparing the allozyme variation of the source fish collected from the Ganaraska River, Ontario to several descendant hatchery lines. Ancestral and descendant rainbow trout do not show significantly different allele frequencies. However, significant differences were detected in brown trout. The absence of several rare alleles in hatchery fish can be explained by sampling error rather than inappropriate propagation methods. Hatchery stocks of either species do not show reduced enzyme heterozygosity compared to wild fish suggesting that the OMNR hatchery system has been successful in retaining allelic variation during broodstock founding and propagation.

Le ministère des ressources naturelles de l'Ontario a mis sur pied, au début des années 80, un programme d'élevage contrôlé dans le but d'obtenir du poisson génétiquement représentatif des populations d'origine. On décrit le plan de gestion des reproducteurs pour la truite brune (*Salmo trutta*) et la truite arc-en-ciel (*Oncorhynchus mykiss*) et on détermine son efficacité en comparant la variation allélique entre le poisson d'origine provenant de la rivière Ganaraska (Ontario) et plusieurs souches de descendants pris dans les piscicultures. Les truites arc-en-ciel d'origine et les descendantes n'accusent pas de différences marquées des fréquences alléliques. Par contre, chez la truite brune on a constaté des différences. L'absence de plusieurs allèles rares dans les poissons d'élevage peut être expliquée par une erreur d'échantillonnage plutôt que par des méthodes de propagation inappropriée. Les poissons d'élevage des deux espèces ne montrent pas d'hétérozygotie enzymatique réduite par rapport aux individus sauvages, ce qui semble indiquer que le programme du ministère a permis de conserver la variation allélique pendant la constitution du stock de reproducteurs et sa propagation.

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The introduction of cultured fishes is a valuable tool for the rehabilitation of natural populations. The success of such introductions in part depends on maintaining the genetic variation of the original wild population in the hatchery fish and minimizing any selective changes to hatchery conditions (Hynes et al. 1981; Allendorf and Ryman 1987). Loss of genetic variability in hatchery fishes may contribute to decreased success once stocked because of reduced adaptive potential (Meffe 1986). For example, more genetically variable rainbow trout (*Oncorhynchus mykiss*) as measured by heterozygosity at enzyme coding loci show superior disease resistance than less heterozygous fish (Ferguson and Drahushchak 1990).

[1]This paper forms part of the Proceedings of the Ecological and Genetic Implications of Fish Introductions Symposium (FIN) convened at the Great Lakes Institute, University of Windsor, Ontario, Canada, May 17–19, 1990.

Reduction of genetic variation in hatchery stocks has been reported in many salmonid species (Allendorf and Phelps 1980; Vuorinen 1982; Cross and King 1983; Ståhl 1983; Gyllensten and Wilson 1987; Verspoor 1988). The loss of genetic variation in hatchery stocks is usually associated with the use of small numbers of fish during initial founding and propagation. Therefore, large effective population sizes are necessary for the minimization of genetic differences between original and hatchery stocks.

Basic principles of population genetics have formed the basis of recommendations for the founding of hatchery populations and the breeding plans in the hatchery stocks after the founding event (Allendorf and Ryman 1987). Despite the acknowledged importance of such genetic principles, there have been few empirical tests of their effectiveness when implemented. The Ontario Ministry of Natural Resources (OMNR) is applying

TABLE 1. Propagation schedule of brown trout at Codrington Fish Culture Station, Ontario. In each year of the program, females from one line (eg. Gn84Ct) were crossed with males from another (eg. GnCt85Ct) to produce a year-class (eg. GnCt88Ct).

Year-class (lot)	No. of families	Year of program								
		81	82	83	84	85	86	87	88	89
Gn82Ct (036)[a]	48	0	1	2	3♂	4♀				
Gn83Ct (039)[a]	32		0	1	2	3♂	4♀			
Gn83ACt (041)[a]	60			0	1	2	3♂	4♀		
Gn84Ct (044)[b]	58				0	1	2	3♂	4♀	
GnCt85Ct (046)	142					0	1	2	3♂	4♀
GnCt86Ct (048)	62						0	1	2	3♂
GnCt87Ct (050	59							0	1	2
GnCt88Ct (052)	60								0	1
GnCt89Ct (054)	60									0

[a]Female and male parents collected from the Ganaraska River.
[b]Female parents collected from the Ganaraska River.

TABLE 2. Propagation schedule of rainbow trout at Normandale Fish Culture Station. In each year of the program, females from one line (eg. Gn83Nm) were crossed with males from another (eg. Gn84Nm) to produce a year-class (eg. GnNm87Nm).

Year-class	No. of families	Year of program						
		83	84	85	86	87	88	89
Gn83Nm[a]	139	0	1	2	3	4♀	5♀	6♂
Gn84Nm[a]	114		0	1	2	3♂	4♂	5♀
Gn85Nm[a]	185			0	1	2	3	4
GnNm87Nm	291					0	1	2
GnNm88Nm	254						0	1
GnNm89Nm	224							0

[a]Female and male parents collected from the Ganaraska River.

genetic principles to the management of the salmonid broodstocks in the provincial fish culture system (Ferguson 1982). We review this comprehensive program and the results of genetic monitoring with rainbow and brown trout (*Salmo trutta*) as examples.

Methods and Materials

Establishment of Broodstocks from Wild Fish

The initial collections of rainbow and brown trout from the Ganaraska River, Ontario were designed so that the founding parents were genetically representative of the original wild populations. Each broodstock was established from sampling a relatively large number of parents (Tables 1 and 2). A founding population of 25 females and 25 males is an absolute minimum to sample the allelic variation of a source population (Allendorf and Ryman 1987). The number of brown and rainbow trout founders well exceeds this minimum (338 and 876 fish, respectively). The founders were sampled over a three year period and throughout the spawning distribution because fish spawning at different times can differ genetically (Leary et al. 1989). Finally, parents were chosen randomly to avoid selection for specific genotypes.

The founding parents were crossed once in single pairs (full-sib families) to ensure that all parents contributed equally to maximize genetic effective population size. Empirical experiments have shown that parents do not contribute equally in pooled gamete matings (Gharrett and Shirley 1985; Withler 1988; Gile 1990; Gile and Ferguson 1990). The full-sib families were incubated separately in individual units until the deposition of eye pigment. Equal numbers of embryos were randomly removed from each family to avoid disproportionate representation of some families.

Propagation of Hatchery Fish

The different year classes (lines) produced from the wild egg collections (first hatchery generation) were reared to maturity and propagated by rotational line crossing (Kincaid 1977) to produce the second hatchery generation (Tables 1 and 2). In each year, a female of one line was mated with a male from another line. In the subsequent year, different sexes of different lines were mated than those used previously. The resulting families were reared separately and contributed equally to the next broodstock generation (at least at the time of sampling) as described previously.

Results

Genetic Monitoring of Hatchery Stocks

We tested the effectiveness of the OMNR broodstock management plan with an electrophoretic analysis of protein coding loci (Allendorf et al. 1977; Leary and Booke 1990) in the founders and derived hatchery fish. The following enzymes showed detectable electrophoretic variation in brown trout from the Ganaraska River: aspartate aminotransferase (sAAT: EC 2.6.1.1), creatine kinase (CK; EC 2.7.3.2), glycerol-3-phosphate dehydrogenase (G3PDH; EC 1.1.1.8), glucose-6-phosphate isomerase (GPI; EC 5.3.1.9), L-lactate dehydrogenase (LDH: EC 1.1.1.27), malate dehydrogenase (sMDH; 1.1.1.37), and mannose-6-phosphate isomerase (MPI; 5.3.1.8). In addition to detectable variation at CK, G3PDH, GPI, LDH, MDH, and MPI, isocitrate dehydrogenase (sIDHP and mIDHP; EC 1.1.1.42), malic enzyme (sMEP; EC 1.1.1.40), dipeptidase (PEPA; 3.4.1.1), phosphoglucomutase (PGM; 5.4.2.2), and superoxide dismutase (sSOD; 1.15.1.1) were also electrophoretically variable in rainbow trout. Allele frequencies and sample sizes are given in Tables 3 and 4.

Temporal Variation in Natural Populations

We first determined with a contingency χ^2 test of allele counts by locus if fish collected from the Ganaraska River in different years differed in allele frequencies (Table 5). This analysis did not include those alleles whose expected counts were less than 5. The duplicated loci (*sMDH-B1,2** [formerly *MDH-3,4*]; *IDHP-3,4**) were each treated as a single locus with four alleles.

Of 8 loci examined in brown trout, only *CK-A1** showed significant heterogeneity in allele counts among fish collected in 1981, 1982, and 1983. Moreover, the combined analysis of all loci indicated no significant differences among collections. Similarly, rainbow trout collected in 1983, 1984, and 1985 showed no detectable genetic differences at 8 loci.

Variation Among Hatchery Lines

A parallel analysis was conducted with three hatchery lines of brown trout and two lines of rainbow trout (Table 5). Even though *MPI** allele counts showed significant differences among lines of brown trout, the combined analysis of all loci was not significant. In rainbow trout, however, allele counts of *sMDH-B1,2** and *SOD**, as well as the combined analysis of all loci indicated that the two hatchery lines differ geneti-

TABLE 3. Allozyme variation in brown trout collected from the Ganaraska River, Ontario and three descendent lots produced at Codrington Fish Culture Station.

		Ganaraska River			Hatchery		
Locus	Allele	1981	1982	1983	GnCt86Ct	GnCt87Ct	GnCt88Ct
AAT-4	100	0.974	0.951	0.949	0.933	0.967	0.949
	85	0.026	0.049	0.051	0.067	0.033	0.051
	N	96	41	79	30	60	59
CK-A1	100	0.880	0.880	0.791	0.800	0.833	0.839
	115	0.120	0.120	0.203	0.200	0.167	0.161
	103	0.000	0.000	0.006	0.000	0.000	0.000
	N	96	71	79	30	60	59
G3PDH-1	100	0.969	0.972	0.924	0.983	0.983	1.000
	−196	0.031	0.028	0.076	0.017	0.017	0.000
	N	96	71	79	30	60	59
GPI-2	100	1.000	0.992	1.000	1.000	1.000	0.992
	145	0.000	0.008	0.000	0.000	0.000	0.008
	N	96	67	79	30	60	59
GPI-3	100	0.948	0.903	0.924	0.983	0.975	0.941
	108	0.052	0.097	0.076	0.017	0.025	0.059
	N	96	67	79	30	60	59
LDH-A2	100	0.972	0.937	0.924	0.900	0.850	0.898
	40	0.028	0.063	0.076	0.100	0.150	0.102
	N	90	71	79	30	60	59
sMDH-A2	100	0.630	0.676	0.576	0.650	0.725	0.669
	152	0.370	0.324	0.424	0.350	0.275	0.331
	N	96	71	79	30	60	59
sMDH-B1,2[a]	100	0.922	0.922	0.921	0.908	0.904	0.919
	80	0.065	0.074	0.076	0.067	0.088	0.068
	116	0.013	0.004	0.003	0.025	0.008	0.013
	N	96	71	79	30	60	59
MPI	100	—	0.806	0.785	0.767	0.725	0.856
	112	—	0.194	0.215	0.233	0.275	0.144
	N	—	49	79	30	60	59
Obs. Het.[b]		0.133	0.156	0.195	0.208	0.181	0.178

[a]Allele frequencies calculated over two loci (4N alleles).
[b]Does not include MPI.

cally. There was no evidence of deviations from random mating proportions in any hatchery lines as no significant deviations from Hardy–Weinberg expectations were detected with χ^2 goodness-of-fit tests of single loci.

Natural Populations and Hatchery Stocks

Counts of specific alleles in the wild collections (years combined) were compared to those in the hatchery lots (lines combined) (Table 5). Both the allele counts of *G3PDH** and *LDH-A2** differed significantly between river and hatchery derived brown trout. The combined analysis of all loci was also significant. In a parallel analysis with rainbow trout, allele counts of *SOD**, differed between river and hatchery fish. The overall statistic for all loci is, however, not significant.

Several rare alleles (frequency $\leq 1\%$) detected in the natural populations were not observed in the samples of hatchery fish. For example, rainbow trout did not have the *CK-A1*76*, *GPI-2*72*, *IDHP-2*90*, and *MPI*115* alleles. Likewise, the *CK-A1*103* allele was not detected in hatchery brown trout.

Finally, the average observed heterozygosity over all polymorphic loci (excluding *MPI** in brown trout) was calculated for each river and hatchery sample. There is no apparent reduction in average heterozygosity within any hatchery line of brown trout (mean river = 0.161; mean hatchery = 0.189) (Table 3) and rainbow trout (mean river = 0.161; mean hatchery = 0.163) (Table 4).

Discussion

The OMNR broodstock management plan has been successful in maintaining the allozyme variation of the source populations of brown and rainbow trout in the hatchery lines; the hatchery lines of both species do not show reduced enzyme heterozygosity relative to the source populations. Moreover, no significant differences in allele frequencies over all loci combined between rainbow trout collected from the Ganaraska River and the descendent hatchery lines at Normandale F.C.S. were detected (not including loci with rare alleles). However, statistically significant differences were detected between wild and hatchery brown trout. The significant deviation between wild and hatchery brown trout over all loci can be attributed to the lower number of founding parents relative to the rainbow trout broodstock. It should be emphasized, however, that the deviation in brown trout, although significant, is limited to only 2 out of 8 loci. This is a relatively small deviation (Allendorf and Phelps 1980; Verspoor 1988).

TABLE 4. Allozyme variation in rainbow trout collected from the Ganaraska River, Ontario and two descendent lots produced at Normandale Fish Culture Station.

Locus	Allele	Ganaraska River			Hatchery	
		1983	1984	1985	GnNm88Nm	GnNm89Nm
CK-A1	100	0.996	1.000	1.000	1.000	1.000
	76	0.004	0.000	0.000	0.000	0.000
	N	263	63	100	62	72
G3PDH-1	100	0.947	0.976	0.945	0.911	0.937
	140	0.053	0.024	0.055	0.089	0.063
	N	263	63	100	62	72
GPI-2	100	1.000	1.000	0.995	1.000	1.000
	72	0.000	0.000	0.005	0.000	0.000
	N	263	63	100	62	72
IDHP-2	100	0.807	0.849	0.815	0.831	0.819
	140	0.193	0.151	0.180	0.169	0.181
	90	0.000	0.000	0.005	0.000	0.000
	N	262	63	100	62	72
IDHP-3,4	100	0.847	0.857	0.819	0.831	0.844
	114	0.037	0.031	0.043	0.040	0.014
	71	0.031	0.045	0.048	0.036	0.056
	40	0.085	0.067	0.090	0.093	0.083
	N	262	56	100	62	72
LDH-A1	100	0.987	1.000	0.990	1.000	0.993
	193	0.013	0.000	0.010	0.000	0.007
	N	263	63	100	62	72
LDH-B2	100	0.996	1.000	0.990	0.992	0.993
	76	0.004	0.000	0.010	0.008	0.007
	N	263	62	100	62	72
sMDH-2	100	0.866	0.904	0.845	0.823	0.889
B1,2[a]	125	0.030	0.020	0.020	0.028	0.014
	83	0.065	0.056	0.085	0.069	0.080
	74	0.039	0.020	0.050	0.081	0.017
	N	250	63	100	62	72
MEP-3	100	0.971	0.960	0.980	0.960	0.986
	75	0.029	0.040	0.020	0.040	0.014
	N	263	63	100	62	72
MPI	100	1.000	1.000	0.990	1.000	1.000
	115	0.000	0.000	0.010	0.000	0.000
	N	263	16	100	62	72
PEP-A1	100	0.966	0.966	0.956	0.944	0.965
	120	0.034	0.034	0.044	0.056	0.035
	N	263	29	90	62	72
PGM-2	100	0.834	0.833	0.850	0.879	0.861
	120	0.011	0.032	0.015	0.008	0.007
	90	0.155	0.135	0.135	0.113	0.132
	N	262	63	100	62	72
SOD	100	0.825	0.770	0.760	0.629	0.813
	152	0.175	0.230	0.225	0.347	0.181
	50	0.000	0.000	0.015	0.024	0.006
	N	262	56	100	62	72
Obs. Het.		0.168	0.148	0.168	0.166	0.160

[a]Allele frequencies calculated over two loci (4N alleles).

In addition to the small number of deviations discussed above, we did not detect several rare alleles in the hatchery lines that were observed in the wild fish. Two explanations that can account for these results are (1) the establishment of the hatchery broodstock was unsuccessful in representing the allozyme diversity of the river fish and (2) the samples sizes for the electrophoretic analysis were too small for detection of rare alleles. The first explanation has negative connotations for the success of the controlled breeding program and therefore it is necessary to determine if the results can be explained by sampling error. We calculated the number of fish expected to be heterozygous for the *CK-A1*76*, *GPI-2*72*, *IDHP-2*90*, and *MPI-2*115* alleles in rainbow trout and *CK-A1*103* in brown trout based on the moderate sample sizes used in this study. In

TABLE 5. Comparisons of genetic differences among samples of rainbow trout and brown trout captured in the Ganaraska River, Ontario, among descendent hatchery lots, and between river and hatchery fish (year-classes and stocks combined). Values are χ^2 statistics (d.f.) from contingency tests of allele counts by locus.

Locus	Comparison		
	Among river samples	Among hatchery lots	Between river and hatchery
Brown trout			
AAT-4	1.624 (2)	1.057 (2)	0.009 (1)
CK-A1	6.220 (2)*	0.454 (2)	0.897 (1)
G3PDH-1	5.333 (2)	–	7.270 (1)**
GPI-3	2.421 (2)	–	3.560 (1)
LDH-A2	4.145 (2)	1.163 (2)	10.240 (1)***
sMDH-A2	3.224 (2)	1.357 (2)	2.857 (1)
sMDH-B1,2	0.003 (2)	0.359 (2)	0.432 (1)
MPI	0.063 (1)	6.201 (2)*	0.013 (1)
Total	23.033 (15)	11.041 (10)	25.278 (8)**
Rainbow trout			
G3PDH-1	2.059 (2)	0.338 (1)	2.041 (1)
IDHP-2	1.187 (2)	0.006 (1)	0.065 (1)
IDHP-3,4	4.538 (6)	3.732 (3)	2.239 (3)
sMDH-B1,2	8.196 (6)	13.687 (3)**	1.377 (3)
MEP-3	1.099 (2)	0.938 (1)	0.001 (1)
PEP-A1	0.405 (1)	0.315 (1)	0.137 (1)
PGM-2	3.310 (4)	0.063 (1)	1.999 (2)
SOD	4.801 (2)	10.409 (1)**	6.167 (1)*
Total	25.595 (25)	29.487 (12)**	14.026 (13)

*$P < 0.05$; ** $p < 0.01$; *** $P < 0.001$.

our hatchery samples, for all loci except one, the number of fish expected with one copy of a rare allele is less than 1 and thus lack of detection because of finite sample size is a reasonable explanation for our data.

The significant differences in allele counts between the two hatchery lines of rainbow trout illustrate why multiple hatchery lines of a single species should be maintained. Even though the two lines were generated from fish collected from the same river and different sexes of the same year-class, genetic differences can arise. The mating of different lines through rotational line crossing is an important method because it will likely reduce such differences.

Unlike the results presented for brown and rainbow trout, hatchery-reared and transplanted lake trout (*Salvelinus namaycush*), and pond-reared walleye (*Stizostedion vitreum*) had significant reduction in genetic variation relative to the wild stocks from which they originated. For example, transplanted lake trout and pond-reared walleye have lost about 36 and 20%, respectively, of their polymorphic loci (Ihssen et al. 1988, unpublished data). The average heterozygosity per locus for lake trout was reduced from 5 to 4.2%. The allelic frequencies of the pond-reared walleye were highly significantly different from those of wild donor populations. Large genetic differences among pond year-classes were observed, whereas repeated samples of the wild founder populations were generally genetically homogeneous. These results can be accounted for by small numbers of wild parents contributing to the pond populations in combination with large variation in survival among pond families.

The genetic similarity between the source and descendent populations of rainbow trout and the small deviations in brown trout in the OMNR hatchery system also stands in marked contrast to other studies with salmonid fishes (Allendorf and Phelps 1980; Vuorinen 1982; Cross and King 1983; Ståhl 1983, 1987; Gyllensten and Wilson 1987; Verspoor 1988). The minor differences between river and hatchery fish could be a function of the relatively recent establishment of the OMNR hatchery stocks in that genetic changes have not had time to accrue. For instance, the genetic changes in westslope cutthroat trout (*Oncorhynchus clarki lewisi*) were detected after the hatchery stock had been established for the longer period of 14 years (Allendorf and Phelps 1980). Cutthroat, rainbow, and brown trout generation times are expected to be similar. However, studies with Atlantic salmon (*Salmo salar*) (Verspoor 1988) suggest that genetic changes are detectable in recently derived stocks. Therefore, our results can be attributed to the OMNR controlled breeding program rather than lack of ability to detect such differences.

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Genetic Interactions Between Hatchery and Wild Salmonids: Lessons from the Pacific Northwest[1]

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The potential for genetic interactions between hatchery and wild populations of salmonids in northwestern North America has increased considerably in recent decades. Efforts to mitigate severe losses to many wild stocks caused by overfishing, destruction of habitat, and blockage of migratory routes have focussed on boosting artificial production in public hatcheries. Opportunities for genetic interactions between hatchery and wild fish will increase if efforts to supplement wild production with hatchery-reared fish continue. Concerns center on three issues: (1) direct genetic effects (caused by hybridization and introgression); (2) indirect genetic effects (principally due to altered selection regimes or reductions in population size caused by competition, predation, disease, or other factors); and (3) genetic changes to hatchery stocks (through selection, drift, or stock transfers), which magnify the consequences of hybridization with wild fish. Strategies for minimizing these genetic risks and monitoring the consequences of various management options are discussed, and some important areas for future research are identified.

La possibilité d'interactions génétiques entre les populations de salmonidés d'élevage et sauvages a augmenté considérablement, ces dernières décennies, dans le nord-ouest de l'Amérique du Nord. Les tentatives pour remédier aux pertes importantes de stocks sauvages en raison de la surpêche, de la perte d'habitat ou du blocage des voies migratoires, ont surtout porté sur l'augmentation de la production dans les pisciculture publiques. La probabilité d'interactions génétiques entre le poisson d'élevage et le poisson sauvage augmentera encore si cet effort se poursuit. On s'inquiète de trois choses : (1) les effets génétiques directs (causés par l'hybridization et l'introgression), (2) les effets génétiques indirects (dûs principalement à des régimes de sélection modifiés ou à des réductions de la taille des populations en raison de la concurrence, de la prédation, de la maladie ou d'autres facteurs), et (3) les changements génétiques du poisson d'élevage (en raison de la sélection, de l'évolution ou des transferts de stocks), qui risquent de grossir les conséquences de l'hybridization avec le poisson sauvage. On parle des stratégies visant à minimiser les risques génétiques et à surveiller les conséquences des différentes options de gestion retenues, et de certains domaines importants de recherche future.

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In the past year, winter run chinook salmon (*Oncorhynchus tshawytscha*) were added to the list of threatened and endangered species in the United States, and the U.S. National Marine Fisheries Service proposed listings for populations of chinook salmon and sockeye salmon (*O. nerka*) from the Snake River. Furthermore, Nehlsen et al. (1991) recently identified a large number of stocks of Pacific salmon they consider to be at some risk of extinction. Dramatic as these events may be, they are only the latest episodes in the century-long decline in abundance of anadromous Pacific salmonids. For example, commercial harvest of chinook salmon in the Columbia River peaked in 1883, declined steadily after 1920, and currently is severely restricted (Mullan 1987). Implications of the initial declines were apparent to many, and by the turn of the century numerous public hatcheries were being operated in an attempt to boost production (Moring 1986; Lichatowich and McIntyre 1987).

Most of the initial declines were due to overfishing, although irrigation projects caused substantial reductions in spawning and rearing habitat in some areas. Dams have also been a major factor in the decline of anadromous salmonids, and nowhere is this more apparent than in the Columbia River Basin, where 19 major dams and scores of smaller projects constitute the world's largest hydroelectric power system (Lee 1989). Grand Coulee Dam (completed in 1941) blocked access of anadromous fish to over 1 800 km of the upper Columbia River Basin, and the Hell's Canyon complex of dams (1958–67) had a similar effect in the Snake River. Fish ladders for returning adults were constructed at many dams, but downstream passage of juveniles through the series of reservoirs and over the dams became a serious problem.

To mitigate losses to anadromous fish caused by the Columbia River dams, the Mitchell Act (1938 and subsequent amendments) directed construction of a series of Federally-funded fish hatcheries. Although some of these hatcheries were successful and make substantial contributions to oceanic fisheries, the abundance of anadromous salmon in the Pacific Northwest continued to decline. In 1980, the U.S. Congress created the Northwest Power Planning Council (NWPPC), with a mandate to develop a program for protection and enhancement of fish and wildlife affected by federal hydroelectric power projects on the Columbia River. The resulting Fish and Wildlife

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Plan (NWPPC 1982, revised in 1984 and 1987) established a goal of doubling the run size of anadromous salmonids throughout the Columbia River Basin. Strategies for achieving this goal include restoration of habitat, reduced juvenile mortality at dams, and substantially increased hatchery production. Significantly, much of the increased hatchery production is intended to come from new facilities in the upper Columbia and Snake River Basins and will involve supplementation of depressed, naturally-spawning stocks with hatchery-reared fish. Similar efforts are underway or are being considered in other areas of the Pacific Northwest.

It is clear from this brief review that there is a long history of looking to hatcheries to make up for the declining abundance of native runs of Pacific salmon and steelhead, *O. mykiss* (see Mahnken et al. 1983). The impact of the hatchery system as a whole has been substantial (Mathews 1980; Washington 1985; Vreeland 1986; Suzumoto and Peltz 1989). The other side of the coin, however, is that hatcheries can also have a substantial impact on native fish. Opportunities for such impacts are certain to become more extensive in the future if supplementation continues to be an important management strategy. Here, I consider some of the possible genetic consequences of artificial propagation of anadromous Pacific salmonids, particularly the effects on native gene pools. Concerns center on three issues: (1) direct genetic effects (caused by hybridization and introgression); (2) indirect genetic effects (altered selection regimes or reductions in population size caused by competition, predation, disease, or other factors); and (3) genetic changes to hatchery stocks (through selection, drift, or stock transfers). In each category, I consider the types of problems that can be anticipated, discuss some of the relevant empirical data, and recommend strategies to minimize the deleterious effects.

Direct Genetic Effects on Wild Fish

Direct genetic effects from hatchery production may occur if cultured fish hybridize with wild fish. Hybridization of different gene pools has two important genetic consequences — loss of interpopulational genetic diversity and outbreeding depression.

Reduction in Between-Population Genetic Variance

Although hybridization typically increases the averge gene diversity (heterozygosity) within the hybridizing populations, it also results in a loss of gene diversity between populations. With salmonids, the concern is that a variety of locally-adapted stocks will be replaced with a smaller number of relatively homogeneous ones (Allendorf and Leary 1988). This process of consolidation tends to limit the evolutionary potential of the species as a whole. Furthermore, different salmonid populations utilize spawning, rearing, migratory, and oceanic resources in a variety of ways and can be expected to show a similar diversity in response to changing environmental conditions. This diversity, therefore, can be expected to buffer total productivity for the resource against periodic or unpredictable changes (Riggs 1990). Events of the past decade, in particular the eruption of Mount St. Helens and the El Niño event of 1982–83, remind us that, on an evolutionary timescale, sudden and drastic change is the rule rather than the exception. Loss of interpopulational diversity thus may lead to a reduction in overall productivity and a greater vulnerability to environmental change.

The strong homing tendency of anadromous *Oncorhynchus* spp. provides a mechanism for local populations to evolve as essentially independent evolutionary units. Although straying is a natural phenomenon and occurs to some degree in most populations that have been studied (e.g., Quinn 1984), fish that stray by substantial distances are relatively infrequent. A number of allozyme studies support the view that genetic differentiation of populations in all species of Pacific salmon and steelhead trout occurs largely along geographic lines (Grant et al. 1980; Parkinson 1984; Beacham et al. 1985, 1987; Wehrhahn and Powell 1987; Utter et al. 1989). Studies of morphology and life-history traits also provide ample evidence for local adaptation (Ricker 1972; Riddell et al. 1981; Taylor 1988; Beacham et al. 1988; Fleming and Gross 1989, 1990).

The principal mechanisms leading to hybridization of hatchery and wild fish are straying of hatchery fish and supplementation of wild populations with hatchery-reared fish. Some data suggest that hatchery fish stray at a higher rate than wild fish, increasing the possibilities for genetic impacts (Ricker 1972; Lister et al. 1981; Withler 1982). Furthermore, if hatchery fish are very abundant, the consequences of straying can be substantial even if the proportion of fish that stray is not high. An extreme example of this is the recent discovery, based on coded-wire-tag data, that in 1989 an estimated 40% of the fall chinook salmon brood stock at Lyons Ferry Hatchery on the Snake River were strays from other hatcheries (C. Busack, Washington Department of Fisheries, pers. comm., April 1991).

Although not considered "strays" in the traditional meaning of the term, cultured fish that are accidentally released (e.g., those that escape from net pens) also may hybridize with wild populations. In Norway, escaped Atlantic salmon already pose a major genetic threat to wild populations (Gausen and Moen 1991), and similar problems may occur in the Pacific Northwest if there is a substantial expansion of net pen farming of *Oncorhynchus* spp. Hindar et al. (1991) discuss this topic in some detail.

It is important to note that the presence of fish in a non-natal stream does not necessarily mean that they breed successfully and leave offspring that survive to reproduce in the next generation. Unfortunately, little information is available on the genetic consequences of straying into natural populations. Reisenbichler and Phelps (1989) suggested that there is circumstantial evidence for the homogenizing effects of hatchery outplants in some steelhead populations. They found that electrophoretic differences among steelhead streams on the Olympic Peninsula are much smaller than those reported by Parkinson (1984) for British Columbia streams. No artificial propagation of steelhead had occurred in British Columbia prior to Parkinson's study, whereas there is a long history of hatchery releases on the Olympic Peninsula.

Outbreeding Depression

Apart from reducing diversity between populations, hybridization can have a variety of effects on fitness of the resulting mixture of gene pools. In some cases, F_1 hybrids display increased fitness known as heterosis, which arises from the masking of deleterious, recessive alleles. Heterosis is more likely if the hybridizing gene pools are inbred and not too different genetically. As genetic distance between the parental stocks increases, however, genetic incompatibilities become more likely and fitness of F_1 hybrids declines. This decline in fitness is known as outbreeding depression. In their study of a

plant species, Wasser and Price (1989) found that levels of outbreeding depression increased with physical distance between hybridizing parents. Unfortunately, little is known specifically about outbreeding depression in salmonids.

Heterosis is presumably possible in the F_1 generation because hybrids retain one entire copy of each parental genome, thus preserving some of the coadapted gene complexes believed to result from local selective pressures (Dobzhansky 1955). With recombination in the F_2 and subsequent generations, however, these genetic combinations are disrupted and shuffled with corresponding parts of the other parental genome. Although there has apparently been no comprehensive, empirical study for any organism of F_2 fitness as a function of genetic divergence between parental stocks, the data that are available almost invariably show lower fitness in F_2 hybrids than in either parental stock (Endler 1977; table 4.6), even if the F_1 generation exhibited hybrid vigor.

Recently, Emlen (1991) developed a model to evaluate the genetic consequences of the hybridization of salmon populations adapted to different environmental regimes. The model allowed Emlen to quantitatively address several key questions regarding hatchery–wild interactions (e.g., What are the genetic consequences of hatchery fish straying into the wild? How does the periodic infusion of wild brood stock into a hatchery affect fitness? and, How much time is required for natural selection to restore fitness in populations that have experienced outbreeding depression?). Given sufficiently different selective regimes for the hybridizing stocks, Emlen concluded that (1) in a scenario involving periodic mixing, non-trivial reductions in fitness may occur even if the mixture proportion is small (5–10%), and (2) recovery of fitness following a single hybridization event may require a large number of generations. This model is potentially useful because it provides a means of dealing with some of the more difficult questions in salmon production; however, there are insufficient data at present to test the accuracy of the model's predictions.

With the renewed interest in supplementation in the last decade has come an increasing awareness of the importance of using hatchery stocks that are genetically compatible with the wild stocks being supplemented. In a number of cases, this has lead to selection of local, wild fish for use in initiating the hatchery brood stock. The logic for this type of program is that artificial propagation can bypass the high early mortality experienced by wild fish, thus providing a large supply of juvenile fish to return as natural spawners. In some programs, hatchery brood stock used in subsequent years includes returning hatchery-spawned fish, whereas other programs use only wild brood stock each year to ensure that no part of the stock is subjected to selection for hatchery conditions for more than a single generation at a time.

Use of local brood stock in supplementation should minimize problems of outbreeding depression, but this approach is not without its dangers. Success of such a program depends on the premise that artificial spawning, propagation, and outplanting can produce more returning adults (with greater reproductive capacity) than could be produced naturally. There are some indications that this is not necessarily the case (Reisenbichler and McIntyre 1986; Seeb et al. 1990). In Idaho, for example, where recent chinook salmon redd counts are generally much lower than pre-1970 counts, the decline has been greater in streams supplemented with hatchery fish than in streams with natural production (Williams 1990). A similar result (decreased natural production in supplemented streams relative to unaffected streams) was found in a more controlled study of coho salmon in Oregon (Nickelson et al. 1986).

The primary danger with this type of supplementation is that if survival of hatchery fish is consistently too low, the hatchery operation acts as a sink for wild brood stock, thus reducing by attrition the very population it was designed to enhance. There is concern that this may be occurring on the Imnaha River in northeastern Oregon, where construction of a facility in 1982 to use local, wild chinook salmon brood stock has thus far produced fewer than one returning adult per adult spawned (Carmichael et al. 1991). Similar problems are being experienced at Sawtooth Hatchery in Idaho (S. Yundt, Idaho Department of Fish and Game, pers. comm., April 1991). These results emphasize the difficulties often encountered in the early stages of a new hatchery operation. Identifying strategies to produce acceptable smolt-adult survival under local conditions may take a number of years, placing the native stock at risk from genetic or demographic effects of reduced population size.

Indirect Genetic Effects on Wild Fish

Reduced Population Size

Any factor that causes a reduction in population size can have an indirect effect on the genetic structure of wild fish populations. Both the total and effective population sizes must be considered in this context. The consequences of low effective population size are discussed in the next section. In general, although reduced effective size has important long-term effects, bottlenecks must be very severe or must last for a number of generations to cause substantial short term increases in inbreeding. In the short term, significant reductions in total size may be more important, as they can seriously disrupt various demographic characteristics of a population and may place it at risk of extinction from severe perturbations in environmental conditions (Soule 1987; Lande 1988).

Some ways in which artificial propagation may lead to reductions in the size of wild populations are widely recognized. For example, Steward and Bjornn (1990) provide a thorough review of studies of the effects of competition, predation, and disease. It is also generally recognized that successful hatcheries can cause other, less direct pressures on wild stock. For example, many mitigation hatcheries have succeeded in increasing the abundance of catchable fish. Apart from the intense social, political, and economic pressures to fully exploit this expanded resource, there is concern that underharvest will result in more hatchery fish escaping to spawn in the wild. However, full utilization of these expanded resources requires increased harvest rates, which in mixed-stock fisheries may place the less abundant (principally wild) stocks at risk (Ricker 1981; McIntyre and Reisenbichler 1986; Lichatowich and McIntyre 1987).

A similar phenomenon may occur with predation on juvenile fish if large numbers of hatchery fish lead to shifts in predator abundance or behavior that increases the predation rate on wild fish (Stewart and Bjornn 1990). This might occur, for example, in reservoirs where predators such as squawfish (*Ptychocheilus oregonensis*) congregate. Predator-prey interactions are generally complex, however, and many scenarios are possible that might lead to unchanged or decreased predation on wild fish as a result of the presence of hatchery fish. More studies are needed in this area.

Other indirect effects on wild fish populations are consequences of making management decisions based primarily

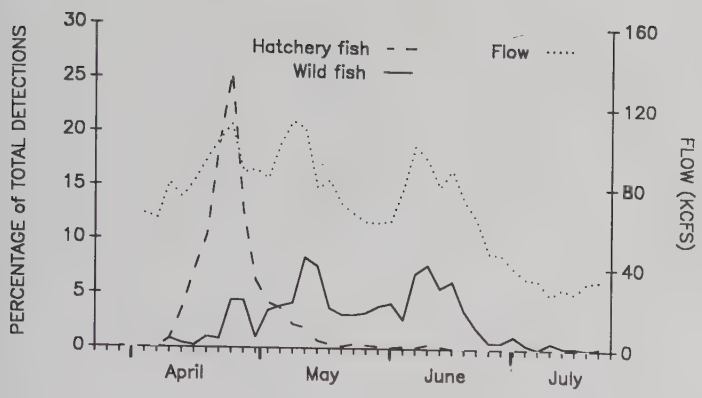

FIG. 1. Passage times through Lower Granite Dam on the Snake River in 1989 for hatchery and wild spring chinook salmon PIT tagged the previous year (Matthews et al. 1990). For each group (hatchery, wild), the percentage of total PIT-tag detections is plotted for 3-day periods. The peak water flows in April and June 1989 resulted from early and late snowmelt, respectively, whereas the peak for 5–13 May represents water released for fish passage.

on information from hatchery fish. For example, obtaining adequate flow through hydroelectric dams to promote juvenile outmigration can be a critical problem in low water years. In the Columbia River Basin, release of water reserved for fish passage generally follows the major releases of fish from upriver hatcheries. Juvenile releases at hatcheries tend to be synchronous and produce large, predictable spikes of hatchery fish at the dams (Fig. 1). In contrast, the outmigration timing of wild stocks, which are sensitive to climatic and environmental conditions, can be much more variable. In 1989, a substantial portion of the wild spring chinook salmon apparently arrived at Lower Granite Dam after the use of the water budget (Fig. 1). For this year, at least, a somewhat later or more prolonged release of water would appear to have been more advantageous for wild fish.

There has also been considerable speculation that oceanic productivity is an important factor in the survival of anadromous salmonids (Salo 1983; Pearcy 1983; Mysak 1986; Nickelson 1986). To the extent that density-dependent factors affect survival (Peterman 1984; Ogura et al. 1989; Emlen et al. 1990), an increase in the abundance of hatchery fish can be expected to reduce success of wild stocks. In this context, Fagen and Smoker (1989) suggested that large-scale hatchery production can be expected to lead to greater fluctuations in abundance in the system as a whole.

Altered Selection Regimes

Any of the above factors that affect the abundance of wild populations can also alter selective pressures and thus cause directional genetic change in wild stocks. Examples include (1) fishing pressure that selectively affects certain size or age groups (Ricker 1981; Nelson and Soule 1987); (2) predation on certain sizes or phenotypes; and (3) flow allocations that favor survival of wild juveniles whose timing of outmigration coincides with that of hatchery fish. Unfortunately, such changes are difficult to demonstrate, and the experiments necessary to do so have not been carried out. Nevertheless, the potential for deleterious effects on wild stocks is real and needs to be considered in managing hatchery operations and planning supplementation programs.

Genetic Changes in Hatchery Stocks

Genetic changes in hatchery stocks are relevant to this discussion because they help to determine the nature and significance of genetic interactions with wild fish. Some of these concepts are covered in detail elsewhere (Gall and Busack 1986; Tave 1986). Important types of genetic change to consider are those due to random processes, selection, and stock mixture.

Random Processes

In populations of small effective size, the erosion of genetic variability through the random extinction of alleles becomes an important consideration. Reductions in overall levels of genetic variability limit the evolutionary potential of a population and may compromise its long-term ability to survive. Furthermore, the erosion of genetic variation leads to an increase in the proportion of individuals that are homozygous for deleterious, recessive alleles, thus reducing fitness through inbreeding depression.

A rich body of population genetics theory deals with these topics, and recent discussions with reference to fishes can be found in Meffe (1986) and Allendorf and Ryman (1987). However, almost all classical population genetics models were developed for organisms with discrete generations, and although many of the basic concepts have been modified for use with age-structured populations, it has not been clear how to apply them to organisms with the complex life history features of Pacific salmon. In particular, a key parameter in most population genetics models is effective population size per generation (N_e), whereas the natural unit of study in *Oncorhynchus* spp. is a single year's spawning population (the remainder of the individuals comprising a generation generally being at sea and logistically unavailable for sampling).

To provide a context for interpreting genetic changes observed in Pacific salmon populations, Waples and Teel (1990) and Waples (1990a) used computer simulations that modeled the unique pattern of semelparity and overlapping year classes in these species. Results indicate that for Pacific salmon, effective population size per generation is equivalent to gN_b, where g is the generation length (average age at spawning) and N_b is the effective number of breeders per year. In a salmon population with N_b breeders per year, genetic variability will be lost at the same rate as in a population with discrete generations and effective size gN_b per generation. However, year-to-year allele frequency fluctuations in salmon populations can be expected to be relatively large because each spawning population represents only a portion of the fish comprising an entire generation. This is important to consider, for example, in interpreting the results of statistical tests comparing genetic parameters in a salmon population at two points in time (Waples and Teel 1990).

Substantial genetic changes and reduced fitness attributed to inbreeding depression have been reported in a number of hatchery stocks of fish (reviewed by Allendorf and Ryman 1987). In the Pacific Northwest, Utter et al. (1989) and Waples et al. (1990) found no trend toward reduced heterozygosities in chinook salmon hatchery stocks in comparison with wild stocks from the same region. However, Simon et al. (1986) presented evidence for a low effective number of breeders in a coho salmon hatchery regularly returning thousands of adults each year. Further, Waples and Teel (1990) and Waples and Smouse (1990) found substantial allele frequency changes and substantial levels of gametic disequilibrium, respectively, in hatchery

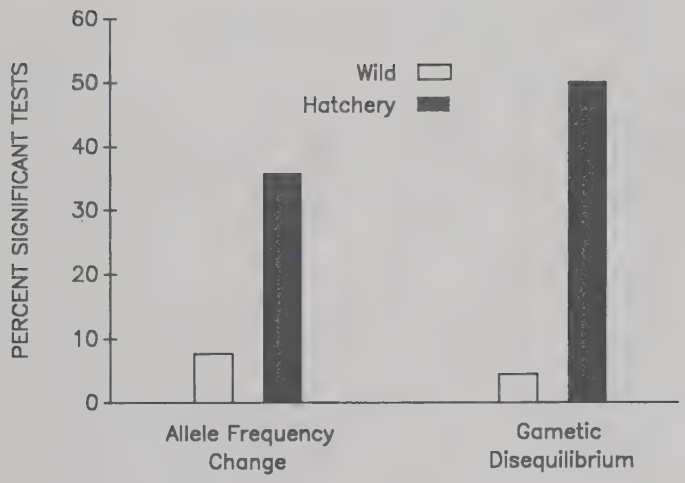

FIG. 2. Percentage of significant chi square tests for gametic disequilibrium and allele frequency change over 2–4 yr in hatchery and wild populations of chinook salmon from the Oregon coast (based on data from Waples and Teel 1990; Waples and Smouse 1990).

(but not wild) chinook salmon stocks from the Oregon coast (Fig. 2). After evaluating a variety of possible causes, the authors concluded that the most plausible explanation for both the disequilibrium and allele frequency change was a low effective number of breeders ($N_b < 50$). Analysis of hatchery brood stock information (Waples and Teel 1990) indicated that a figure in this range is possible for many of the hatcheries included in the study.

Selection

In stocks that are permanently cultured, genetic changes mediated by selection (natural or artificial) are inevitable and, to a certain extent, may be desirable. For example, in a cultured freshwater species such as rainbow trout, genotypes that are well adapted to conditions in the hatchery environment can be expected to increase at the expense of those that fare poorly. If we ignore possible problems associated with inbreeding, disease, etc., this process should lead to increased fitness and higher productivity of the population in the hatchery environment.

Selective regimes are different in anadromous species, for which the hatchery environment represents only a portion of the life cycle. The main advantage to artificial propagation of anadromous species is that a large percentage of fertilized eggs can be raised to fry or smolts, thus avoiding the heavy early mortality experienced by wild populations. Barring a major disease outbreak, egg/smolt survival in salmon hatcheries is generally 50% or higher, as opposed to generally under 10% for wild populations (e.g. Howell et al. 1985). This high in-hatchery survival rate, however, means that much of the culling that occurs before the fish return as adults takes place outside the hatchery environment. Post-release mortality of hatchery *Oncorhynchus* spp. often exceeds 99% for some species (e.g. Howell et al. 1985), much higher than the figure for most wild stocks that have been studied.

As a result, the pattern of mortality in hatchery stocks is very different from that experienced in the wild (Fig. 3). These differences suggest that there are substantial opportunities for selection to change the genetic characteristics of hatchery stocks from those of the donor wild stocks. To see this, consider two populations: a wild one and a hatchery stock derived from it.

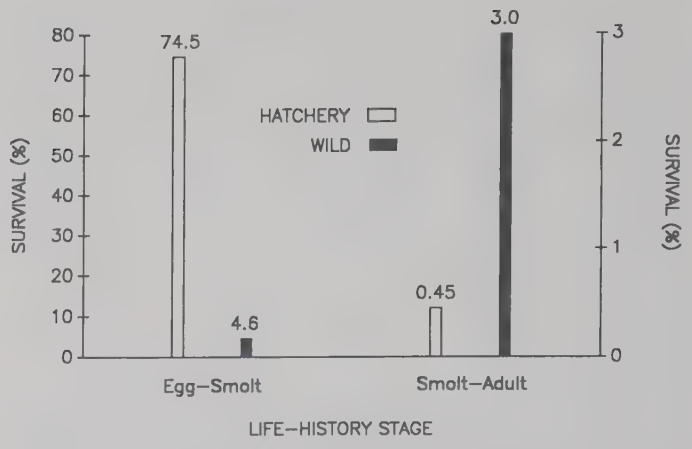

FIG. 3. Egg-smolt and smolt-adult survival of hatchery and wild spring chinook salmon from the Deschutes River, Oregon. Wild data are for brood years 1975–81; hatchery data are for brood years 1977–83 at Warm Springs and Round Butte Hatcheries (Lindsay et al. 1989). Mortality in nature is difficult to measure, so values for the wild population should be regarded as approximate. Although survival rates can be expected to vary somewhat among populations and species, the shift in pattern of mortality to a later-history stage is typical of cultured populations of anadromous salmonids.

Most of the fish raised to smolts in the hatchery population would not have survived in the wild; conversely, a higher percentage of hatchery smolts typically do not survive to return as adults. Directional genetic change, causing the hatchery stock to diverge from the wild stock, will occur unless either (1) all mortality (hatchery and wild) is completely random with respect to genotype; or (2) the fish representing the excess hatchery mortality in the smolt-adult phase are genetically equivalent to those representing the excess hatchery survival in the egg-smolt phase. I would argue that scenario (1) is not plausible and scenario (2) is also highly unlikely. The higher egg-smolt survival in the hatchery must, to a certain degree, represent a relaxation of selection that occurs in the wild, and there is little reason to believe that processes occurring after release from the hatchery will exactly compensate for this effect. We are thus led to the conclusion that, in general, selective pressures will cause hatchery fish to diverge genetically from a donor wild stock. Such opportunities may be somewhat more limited for chum and pink salmon, which are released as fry and thus spend a shorter time in the hatchery than do most coho or chinook salmon or steelhead.

It is not clear, however, to what extent these genetic changes can be expected to result in "rapid selection for an optimal 'hatchery type' fish" (Helle 1981, p. 1668). This may be true for species that can be cultured throughout the entire life cycle, but the outcome is less clear for anadromous species. Certainly there are opportunities for domestication selection prior to release, and there is some evidence that hatchery fish may perform better than wild fish in the hatchery environment (e.g. Reisenbichler and McIntyre 1977). However, the high post-release mortality rate for hatchery fish means there is also considerable opportunity for selection against traits that are adaptive in the hatchery environment but not in the wild. Again, a variety of scenarios is possible, but unless genotypes positively selected for in the hatchery are neutral or advantageous in the wild, there will be a tendency for counteracting selection in the smolt or fry to adult phase. Because of alternating (and likely conflicting) selective regimes, selection for hatchery-adapted

traits should not be as efficient in anadromous species as it is in species that spend their entire life cycle in captivity. Although directional genetic change (relative to a wild donor stock) can be expected in an anadromous hatchery stock, the nature of such changes must be to a certain degree unpredictable.

Thus far we have considered only "natural" selection that occurs in the hatchery environment and in the wild. There are also ample opportunities for artificial (directed or inadvertent) selection in cultured populations. In particular, the selection of which fish will breed in captivity differs in so many basic ways from the process that occurs in the wild that genetic change relative to the wild stock is almost inevitable. Efforts to choose brood stock according to age, time of return, or phenotypic characters such as size are well documented (e.g. Donaldson and Menasveta 1961). One of the more common occurrences in hatcheries of *Oncorhynchus* spp. is advancement of time of spawning, which results in part from failure to spawn late-returning fish because the egg-take quota has been filled. There is evidence that time at spawning is genetically controlled in Pacific salmon. For example, Lane et al. (1990) found that a genetic mark introduced into the late part of a pink salmon run in Alaska was still detectable after four generations only in fish returning near the end of the spawning period.

Time of spawning may have particular importance for steelhead, which reproduce in the spring. In wild populations, early spawners may have reduced success because of unpredictable environmental conditions or other factors (Cederholm 1984). In the relatively constant hatchery environment, however, selection against early spawning is relaxed. In fact, because early spawning tends to produce fish that are larger at release or can be released earlier (and therefore may survive better), this trait may be positively selected for in the hatchery, and active efforts may be necessary to counteract the trend (Reisenbichler and McIntyre 1986). To the extent that spawning time is shifted in hatchery stocks, it can be expected to reduce fitness of hatchery fish or hatchery-wild hybrids that spawn in the wild.

Even if efforts are made to avoid artificial selection of brood stock (e.g., by mating all returning adults or a random sample thereof), genetic changes can be expected in the hatchery because of the impossibility of mimicking natural selection for reproductive success. In wild populations, which individuals mate (and with what success) is determined by a variety of factors we are just beginning to understand. Fleming and Gross (1989) showed that phenotypic traits associated with female mating success in coho salmon were reduced in hatchery stocks, presumably due to relaxation of breeding competition. This raises concerns about the ability of hatchery-reared fish to produce viable progeny in the wild and may help explain reports (e.g. Leider et al. 1990) of reduced reproductive success in the wild of transplanted hatchery fish.

Stock Mixtures

The genetic consequences of stock mixture have been described above. Transfer of fish and eggs among salmon hatcheries has been a common practice for over 100 years. Often, these historical mixture events can be detected as homogeneity of geographically distant populations. For example, several widely separated spring chinook salmon hatcheries in the Columbia River (Carson, Leavenworth, Little White Salmon, Winthrop) are genetically homogeneous based on electrophoretic characters (National Marine Fisheries Service and Washington Department of Fisheries, unpubl. data). The Carson–Leavenworth stock has been used in each of these hatcheries, as well as in several others in the Columbia and Snake River drainages. This practice tends to replace a variety of stocks with a few generic types. Furthermore, as the geographic distribution of genetically homogeneous hatchery stocks widens, the potential for harmful genetic interactions with genetically distinct wild stocks increases.

Recommendations

From the preceding discussion, two things should be clear: (1) hatchery fish can have substantial direct and indirect genetic impacts on wild fish, and (2) the only sure way to avoid these problems is to "Just say No" — to stock transfers, supplementation, and artificial propagation of any kind. Given that (2) is not a realistic scenario, at least in the near future, it is important to identify strategies to minimize the adverse genetic consequences of artificial propagation. Unfortunately, at present we are in a better position to identify the potential dangers than to provide explicit guidelines for dealing with the problems. Nevertheless, there is increasing pressure on resource managers to make practical decisions that may have profound consequences, and it is important that these decisions be informed ones. In that spirit, therefore, the following suggestions are advanced regarding some of the major concerns for genetic interactions of hatchery and wild stocks.

Supplementation

Considering the importance of diverse, native gene pools to the long-term survival of the Pacific salmon species, management efforts should focus on ensuring that depressed wild stocks reach adequate, sustainable escapement levels without (or in spite of) the aid of hatcheries. That is, instead of trying to mitigate losses to wild stocks through expanding hatchery operations and refining hatchery technology, resources should be directed toward fixing the problems that caused the declines in the first place (Francis 1990).

Unfortunately, such measures will not always be feasible. As an alternative, supplementation of depressed, naturally spawning populations with hatchery-reared fish is an attractive concept on paper. In practice, however, this technique has seldom been successful in achieving the objective of increased natural production (Steward and Bjornn 1990; but see also Cuenco 1991). The genetic consequences of supplementation programs have also been quite varied. In recent reviews, for example, Skaala et al. (1990) and Hindar et al. (1991) cited examples in which the native stock had been largely or entirely displaced, examples of hybridization between native and hatchery fish, and examples in which repeated hatchery releases had no detectable genetic effect on the native population.

This unpredictability, coupled with the potentially severe consequences of mixing diverse gene pools, mandates that the ramifications of proposed supplementation programs be carefully considered before implementation. Riggs (1986, 1990) has suggested a framework within which proposed programs can be evaluated. This framework recognizes that a variety of different management opportunities exist and that each is appropriate under certain circumstances (Table 1; see also Francis 1990 for an alternative set of guidelines). In general, strategies with low genetic risk to the local stocks (e.g. no supplementation or use of local brood stock) should be adopted if the local stocks have previously had little or no hatchery influence, whereas high-risk strategies (e.g., introduction of a new

TABLE 1. Framework for evaluating different enhancement options in terms of opportunities for conserving genetic resources of wild/natural populations of anadromous salmonids (after Riggs 1986, 1990). Either of two options may be chosen when wild and hatchery stocks coexist (Scenario C).

Scenario	Preferred option(s)
A No previous hatchery influence	Retain native gene pools
B Little previous hatchery influence	Facilitate wild & natural productivity
C Wild and hatchery stocks coexist	Facilitate wild & natural productivity (minimize hybridization) or Facilitate hatchery naturalization (integrate hatchery/wild production)
D Little wild/natural production	Facilitate hatchery productivity
E No native stock remains, or introduced stock performing poorly	Test a new stock

stock) may be acceptable in cases where suitable habitat does not support fish or existing introduced stocks are performing poorly. In developing a management strategy, therefore, the first step is to identify the option or options that result in an acceptable degree of genetic risk, given the status of and likely consequences to the local stocks. Strategies that are deemed inappropriate within this framework should be considered only after a full public discussion. In some cases, the mandate of the U.S. Endangered Species Act to protect native populations may dictate the appropriate management option (cf. Waples 1991).

In rare situations, more extreme measures may be appropriate. For example, inbreeding depression in a stock that has gone through a genetic bottleneck may be alleviated by infusion of new genes from another population. The results of such a strategy, however, are highly unpredictable, and this option should be considered only after exhausting other possibilities. Similar caveats apply to the suggestion of Krueger et al. (1981) that release of numerous stocks in an unutilized habitat and allowing selection to filter the resulting genetic combinations may produce some that are well adapted to the local environment.

The recent shift toward use of locally-adapted stocks to initiate hatchery stocks used in supplementation has been a welcome change from previous tendencies to widely disseminate a select few stocks. Periodic infusion of wild brood stock into the hatchery may also help to prevent genetic divergence of the hatchery and wild stocks. However, evidence that this type of supplementation actually works is scant. At present, results of such programs can at best be described as unpredictable. The prospect that the "supplementation" program will evolve into a program of mining wild brood stock to support the hatchery is very real.

In considering such a supplementation program, a guiding principle should be, "First, do no harm." That is, supplementation should be considered only if there is adequate assurance that it will not make the problem worse. Given the aforementioned lack of predictability in enhancement programs, most such efforts should probably begin as small-scale research studies to demonstrate the feasibility of proposed actions. An adequate monitoring program should be an integral part of any supplementation effort. Biological and genetic characteristics should be monitored over time to track the consequences of supplementation. Intentional genetic marks (Gharrett and Seeb 1990; Utter and Seeb 1990) may be considered if the hatchery stock cannot reliably be distinguished from the target population with existing genetic markers — as may be expected if local brood stock are integrated into the hatchery program. Permanently marking an entire population may entail some risks that should be carefully considered before this course is adopted. The technique, however, is particularly well suited for research studies in which only a portion of the population will be affected. Seeb et al. (1990) describe a study in which genetic marking was used to evaluate productivity of a supplemented population.

It is also crucial to be able to distinguish hatchery from wild fish as adults return to spawn. In North America, most hatchery steelhead are adipose fin-clipped (Light 1989), but this is often not the case with other species. The Sawtooth Hatchery in Idaho provides an example of the types of problems that can result from the inability to separate hatchery and wild fish. The chinook salmon stock at this hatchery was initiated from local Salmon River fish destined for spawning grounds upriver from the hatchery. Each year, about two-thirds of the adults reaching the hatchery weir are taken into the hatchery to spawn, the remainder being allowed to pass above the weir to spawn naturally. Although all fin-clipped adults are taken into the hatchery, only a small percentage of the fish released from the hatchery are so marked, so many hatchery fish undoubtedly are allowed to pass above the weir. More importantly, the proportion of the wild run that is intercepted each year is not known. There are some indications of poor adult returns to the hatchery, suggesting that wild fish may be supporting the hatchery program (J. Williams, National Marine Fisheries Service, pers. comm., May 1990). Uncertainty surrounding the situation at Sawtooth emphasizes the importance of an adequate monitoring program.

Finally, more research is needed to understand the effects of hybridization between different salmon stocks. At present, all we can say is that outbreeding depression is an important consideration, and the magnitude of the problem probably increases with increasing differences between populations. A carefully designed experimental program may identify measurable attributes of natural populations that allow predictions regarding outbreeding depression. Such a research program may also identify circumstances under which interpopulational hybridization is unlikely to be a problem, and perhaps may even be beneficial.

Indirect Effects of Hatchery Fish

Many of the indirect genetic effects of hatcheries result from the temporary presence of large numbers of juvenile hatchery

fish in the riverine system. The abundance of such fish may in some cases exceed historical estimates of the total number of juveniles produced in the wild. For example, Raymond (1988) estimated that in 1964–68, 1.3 to 2 million chinook salmon smolts in the Snake River system produced about 50 000 – 80 000 returning adults, whereas upwards of 10 million smolts are currently released by Snake River hatcheries alone and total adult production (hatchery and wild) is perhaps one-third as large as in 1964–68. Several new Snake River dams built since the 1960's have undoubtedly contributed to the declining returns, but the possibility that the river cannot support 10 million smolts (particularly if most are released at about the same time) must also be considered. An obvious alternative that merits serious consideration is to release fewer, instead of more, hatchery fish (Walters 1988).

A major impediment to such an approach is that hatchery performance has traditionally been evaluated in terms of juvenile production. Hatchery managers thus have considerable incentive to increase rearing density as long as juvenile mortality does not suffer and overt disease symptoms do not appear. The resource as a whole, however, would be better served if more emphasis were placed on smolt quality (rather than quantity) and on adult production (fishery contribution + spawning escapement), which is after all the end result we all seek. Shifting emphasis to adult production will require monitoring programs that presently exist for some but not all hatcheries.

In a broader view, the success of hatchery operations can properly be evaluated only with reference to success of the hatchery-wild system as a whole. The complexities of the marine environment and possible density dependent effects also have to be considered in this context.

Genetic Changes in Hatchery Stocks

Directional genetic changes resulting "naturally" from the hatchery environment are probably inevitable, perhaps even desirable in permanently cultured populations. Random changes, however, are unlikely to be beneficial, and artificial selection can produce genetic change that reduces the ability of the stock to survive and reproduce in the wild. Brood-stock protocols designed to minimize these types of genetic change have been discussed elsewhere (e.g. Simon et al. 1986; Allendorf and Ryman 1987). In practice, however, some procedures may seem difficult or costly to implement exactly as recommended. What is needed, therefore, is not just an idealized set of guidelines, which may be disregarded entirely if deemed too onerous, but a practical handbook that recognizes contingency situations likely to occur in hatcheries and provides alternative measures that produce acceptable results under difficult circumstances.

Even if such protocols are followed, however, there is no guarantee that inbreeding effects and random genetic changes will be as small as desired. The principal reason for this is that these factors depend on effective population size, which is strongly affected by the variance among individuals in reproductive success — a parameter that is very difficult to measure in natural populations. If this variance is large, the effective number of breeders (N_b) may be much smaller than the actual number (N). In a captive brood-stock program, reproductive output of different families can be equalized, thus preventing a substantial decline in effective size relative to the number of spawners used. This is not possible with anadromous species released as juveniles, because mortality following release is typically very high and may differ substantially among families. One solution is a systematic program to monitor genetic changes over time, the magnitude of which provides an indication of effective size and the likely incidence of inbreeding (Waples 1990b). In this way, it may be possible to identify hatcheries in which efforts to maintain an adequate effective size are not working, thus permitting corrective action before serious problems associated with inbreeding arise.

Concurrent with efforts to maintain genetic variability in hatchery populations, experiments should be designed to study factors affecting reproductive success in the wild. At present, given that we cannot mimic a natural mating process we don't fully understand, the best hatchery breeding strategy seems to be to use a large enough, approximately random sample of adults that artificial selection and stochastic changes are minimized. A full appreciation of the genetic consequences of artificial propagation cannot be achieved until we better understand the determinants of fitness in the wild.

Conclusion

The recommendations above can act as guiding principles in determining the genetic effects of artificial propagation of anadromous Pacific salmonids. It is hoped they will provide a means for achieving consensus regarding appropriate management options. Too often, the debate has been cast in terms of production vs. genetics. Perhaps the most important message to be derived from the above is that in the long term, production and sound genetic principles are inseparable. This is articulated in the Draft Principles for Genetic Conservation and Production Quality (Riggs 1990; p. 3):

> Given that (a) Pacific salmon represent a unique resource of great cultural, social, and economic value, and that (b) this resource is the product of many thousands of years of evolution, therefore responsible public policy should not be driven solely by short term considerations. Rather, as stewards of the resource, all responsible parties should seek ways to ensure that the resource is available for many generations to come. Purposeful planning to assure the quality and effectiveness of production activities must acknowledge that sustained production and long-term health of the resource can be achieved only by conserving the genetic information in this evolutionary legacy.

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Loss of Exploited, Indigenous Populations of Lake Trout, *Salvelinus namaycush*, by Stocking of Non-Native Stocks[1,2]

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A deterministic, age-structured population model was developed to explore the combined effects of exploitation and stocking of hatchery-reared lake trout on native lake trout populations. Stocking of non-native lake trout at moderate to high exploitation rates caused loss of the recipient population, even when the stocked fish did not reproduce or interbreed with the native fish. If hatchery fish reproduce, their progeny mask the loss of the wild stock. At exploitation and stocking rates typical of lake trout populations in Ontario, the wild stock was replaced by the hatchery stock in a few generations. Native stocks having weak recruitment are least resistant to displacement by hatchery stocks and are also the most likely to be subjected to stocking. Evidence from several field studies in Ontario generally provided support for our stock displacement hypothesis and modelling results. Extensive stocking of a few domesticated hatchery stocks has the potential to reduce genetic heterogeneity through loss of locally adapted stocks of lake trout. We suggest that emphasis should be placed on protecting the genetic integrity of the remaining self-sustaining wild stocks, and that a moratorium be considered on supplementation stocking of these populations, especially with non-native hatchery-reared stocks.

On a mis au point un modèle déterministe fondé sur l'âge d'une population pour étudier les effets combinés de l'empoissonnement avec des touladis d'élevage et de l'exploitation sur des populations de touladis indigènes. L'empoissonnement avec des touladis non indigènes, combiné à des taux d'exploitations moyens à élevés, a provoqué la disparition de la population originale, même lorsque les poissons introduits ne se sont pas reproduits entre eux ou ne se sont pas croisés avec les poissons indigènes. Si les poissons d'élevage se reproduisent, leur progéniture masque la disparition du stock naturel. Aux taux habituels d'exploitation et d'empoissonnement observés pour les populations de touladis en Ontario, le stock naturel a été remplacé par le stock d'élevage après quelques générations. Les stocks indigènes ayant un faible recrutement sont déplacés plus facilement par les stocks d'élevage et sont également les plus susceptibles de faire l'objet de mesures d'empoissonnement. Des données provenant de plusieurs études sur le terrain effectuées en Ontario confirment généralement notre hypothèse sur le déplacement des stocks et les résultats de notre modélisation. L'empoissonnement intensif avec quelques stocks de poissons d'élevage peut causer la disparition des stocks de touladis adaptés aux conditions locales et réduire ainsi l'hétérogénéité génétique. Nous recommandons que l'accent soit mis sur la protection de l'intégrité des stocks naturels viables qui restent et que soit considérée la possibilité d'imposer un moratoire sur l'empoissonnement d'appoint dans le cas des populations indigènes, particulièrement lorsque les stocks introduits sont composés de poissons d'élevage non indigènes.

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Loss of genetic diversity has been recognized as an important fisheries management issue for some time (Loftus 1976; Ryman 1981; Ryman and Ståhl 1981; Meffe 1986), and has become an ecological issue of global significance (Myers 1984). Dramatic loss of genetic diversity occurs when species or locally adapted subpopulations or stocks are lost through catastrophic or demographic extinctions. The latter, involving the gradual decline in a breeding stock to critically low numbers of individuals, can be caused by progressive habitat loss, exploitation, and other anthropogenic influences. More subtle loss of genetic diversity can be caused by partial or complete replacement of one species or stock by a conspecific or closely related species through introgressive hybridization (Busack and Gall 1981; Whitmore 1983; Campton and Johnston 1985), or by simple numerical replacement of one stock by another. Zoogeographic manipulations of fish species by humans, including species transplantation, introduction of exotic species, and supplementation stocking of hatchery-reared stocks, comprises a rich source of information for investigation of the effects of species and population interactions on genetic diversity.

Supplemental stocking of hatchery-reared fish stocks, which is the subject of this study, involves the introduction of a spe-

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cies into a water body that is already occupied by a self-sustaining population of the same species. Usually, the objective is to supplement or enhance a depleted population, either to rehabilitate a local stock or to sustain harvests at levels commensurate with a partially regulated fishing demand. Stocking of this type usually occurs in conjunction with high levels of fishing exploitation, that ultimately may have been responsible for depletion of the native stock in the first instance, although other factors, such as habitat degradation, are also often implicated. Supplemental stocking of non-native stocks is a common management practise in North America. In Ontario for example, 1827 lakes are inhabitated by native lake trout, *Salvelinus namaycush*, stocks and 341 of the 352 that have received supplemental stocking have involved non-native stocks (Evans et al. 1991a). In total, therefore, 18.7% of the wild self-sustaining lake trout populations in Ontario have been stocked with lake trout of non-native origin, while only 0.6% have received lake trout of native parental origin.

Supplemental stocking of lake trout populations, with hatchery-reared stocks, raises two main concerns about the possible interactions between wild and introduced hatchery fish: (1) the effects of possible introgressive hybridization on the genetic structure of the recipient native population; and (2) the risk of numerical displacement of the native stock by the hatchery stock when the artificial recruitment (stocking) rate exceeds the natural recruitment rate. Replacement of wild native stocks with non-native stocks, should this occur by either interbreeding or numerical displacement, would tend to lower the diversity of the species if there is loss of locally adapted stocks.

Our specific objective was to investigate the combined effects of exploitation and stocking of hatchery-reared lake trout on the stock composition of partially self-sustaining lake trout populations. Two main hypotheses were tested: (1) stocking of hatchery-reared lake trout results in the loss of native stocks, even in the absence of reproduction of the hatchery fish; and (2) high fishing mortality accelerates the rate of displacement of native lake trout stocks by hatchery stocks. These hypotheses were investigated using a simulation model of lake trout population dynamics, and by evaluation of changes in stock composition during the 24 and 38 yr histories of supplemental stocking of hatchery-reared lake trout in lakes Simcoe and Manitou, Ontario. We also reviewed the responses of 13 smaller Ontario lakes to lake trout stocking.

We evaluated the effect of stocking hatchery-reared lake trout under two reproductive scenarios: (1) a scenario in which hatchery-reared lake trout fail to reproduce in the presence of native trout (equivalent to reproductive sterility of the hatchery fish); and (2) a scenario in which native and hatchery trout reproduce successfully, but do not interbreed because of behavioural reproductive segregation.

Materials and Methods

Lake Trout Population Model

An age-structured, deterministic population model was developed, to explore changes in stock composition caused by stocking of non-native lake trout on naturally reproducing, indigenous lake trout populations. The model has features specific to piscivorous lake trout populations in Ontario, including growth rate and maturation schedules, and is based largely on the Lake Opeongo lake trout population and angling fishery, for which a 50 yr history is available (Martin and Fry 1972; Shuter et al. 1987).

The model incorporates a density-dependent recruitment function, which simulates regulation of recruitment through cannibalism by adult lake trout on juveniles aged 1 to 3 yr. Several observations of cannibalism in wild lake trout populations (Martin and Olver 1980; Johnson 1976), and spatial segregation of adult and juvenile lake trout during summer (Evans et al. 1991b), suggests that cannibalism is an important phenomenon in piscivorous lake trout populations, although Martin and Olver (1980) and Johnson (1976) attributed only minor significance to it. Mean fork lengths of Lake Opeongo lake trout at 1, 2 and 3 yr, back-calculated from scales for the period 1941–71 were 48.6 ± 1.9, 96.2 ± 3.2 and 148.4 ± 4.9 mm (± SD), respectively (Matuszek et al. 1990), which are well within the size range known to be cannibalized by adult trout (Harper 1948; Frantz and Cordone 1970). The standing stock of fish aged 1–20 yr in each year is based on the number of fish alive at the end of the preceding year. Egg production was a simple function of the biomass of adult females aged 6–20 yr. For present purposes, we have assumed that adult lake trout of wild and stocked origin are similarly predisposed to preying on young lake trout.

Field evidence indicates that juvenile, hatchery-reared lake trout experience greater cannibalism mortality than their wild counterparts (Martin and Olver 1980; MacLean et al. 1981). To accommodate possible differential juvenile survival of wild and hatchery trout, our model provides the option of discounting the annual survival of the hatchery-reared juveniles to any fraction of that derived from the stock-recruitment function for the wild juveniles.

Model Description and Rationale

The computer model was developed to simulate the effects of fishing and stocking on wild, native lake trout populations. The model was parameterized using the Lake Opeongo stock-recruitment relationship and does not allow for lake area or productivity adjustments, therefore, the level of recruitment corresponds to a hypothetical lake with area and productivity equivalent to Lake Opeongo. A Ricker-type stock-recruitment function was used to determine the survival rates of juvenile trout (ages 1, 2 and 3 yr) as a function of the abundance of all adults age 6 yr and older.

The model accommodates natural recruitment of wild trout, stocking of hatchery-reared yearling lake trout, and natural recruitment from hatchery trout. The model does not accommodate hybridization between first-generation hatchery-reared lake trout and wild lake trout. Survival of wild and stocked trout was tabulated separately, but the combined abundance of adult trout of wild and hatchery origin was used to determine the survival rates of the 1, 2 and 3 yr-olds of wild and hatchery origin. Two reproductive scenarios were simulated:

1) natural reproduction of wild trout, but no reproduction of hatchery trout;
2) natural reproduction of wild and domestic trout; survival from egg to age 1 yr was set independently and at any desired level for the wild (S_{wo}) and hatchery fish (S_{no}).

Under reproductive scenario 2, natural progeny of hatchery trout (ages 1 and greater) were combined with the progeny of wild trout, because they would not normally be distinguishable in the field (Marsden et al. 1989). At present, there is no published information about the extent of interbreeding between wild and hatchery lake trout. In all cases, in which first-generation hatchery fish reproduced, we assumed complete mixing

and interbreeding between their progeny and the wild fish. Fin-clipped, first generation hatchery fish, however, were restricted to breeding only with fish of hatchery origin, in order to simplify the number of reproductive scenarios. Some field evidence suggests that this type of segregation occurs among first-generation hatchery stocks in Lake Simcoe, Ontario (MacLean et al. 1981).

Model Structure

Following the usual convention for age-structured population models, the numbers of fish in each successive age-class were computed from:

$$(1) \quad N_{i+1,t+1} = N_{i,t}e^{-(F+M)}$$

where $N_{i,t}$ = number of fish in age class i in year t
F = instantananeous rate of fishing mortality
M = instantaneous rate of natural mortality
$F + M = Z$ = instantaneous rate of total mortality
and $N_{i+1,t+1}/N_{i,t}$ = rate of survival

The population structure in year zero was set at the beginning of each simulation. Instantaneous rates of fishing (F) and natural (M) mortality were determined separately for three discrete life stage intervals: egg to age 1 yr, juveniles (age 1–3 yr) and adults (4–20 yr).

Fishing mortality (F) was zero for ages 0–3 yr. All fish 8 yr of age and older were assumed to be fully recruited to the fishery, wheres ages 4–7 yr were assigned partial vulnerabilities as estimated for Lake Opeongo lake trout as follows, using the methods of Shuter et al. (1987):

Age	Instantaneous rate of fishing mortality
4	.12 * F
5	.30 * F
6	.57 * F
7	.75 * F
8 and older	F

Natural mortality for fish age 0 (M_0) and 4–20 yr (M_2) was independent of density, while a Ricker-type density dependent mortality function was fitted to data reported by Payne et al. (1990) and applied to juvenile lake trout ages 1–3 yr (a 3-yr period) as follows:

$$(2) \quad S_{1-3} = a\, e^{-BP_A}$$

where S_{1-3} = survival age 1 to age 3 yr
P_A = total biomass of fish age ≥6 yr
$a = 0.900$
$B = 0.00016$

This function is similar to the density-dependent survival function of Matuszek et al. (1990) assuming egg production to be 1600 eggs kg^{-1} mature female (Martin and Olver 1980). To convert to an annual instantaneous mortality rate, we took the natural logarithm and divided by 3 yr as follows:

$$(3) \quad M_1 = [(-0.00016P_A) - 0.10536] / 3$$

where M_1 = the instantaneous natural mortality rate for ages 1, 2 and 3 yr.

Instantaneous natural mortality of the juveniles was not allowed to fall below 0.10, even though lower values were determined by the recruitment function. This prohibited annual survival of juvenile fish from exceeding about 90%. We assumed that at low densities of adult trout, other mortality factors, such as predation or competition by other species, would check survival rates. Survival of first generation hatchery juveniles (S_{hj}) was set as some fraction of the survival of wild juveniles from 0 (no survival) to 1.0 (the same as the wild juveniles). Field observations suggest that hatchery-reared juvenile lake trout suffer an initial high post-stocking mortality. The model allows for incorporation of this mortality. Survival of hatchery juveniles is coded as a fraction of the wild juveniles (e.g. $S_{hj} = 0.8$ indicates that survival of hatchery juveniles has been discounted by 20% relative to the wild juveniles).

Age 4 and older

The Lake Opeongo fishery operates during spring and summer months only. Stocks supporting both summer and winter fisheries would be expected to suffer higher mortality at younger ages, because of the tendency of winter fisheries to capture smaller and younger fish (Martin 1954; Evans et al. 1991a). Our model, therefore, provides a relatively conservative response to the effects of fishing. Natural mortality of the older juveniles and adults (M_2) was constant at 0.10 for all fish aged 4–20 yr.

Growth and Egg Production

The von Bertalanffy equation, based on a mean for Ontario lake trout populations, was used to determine fork length (FL) (cm) as follows:

$$\mathrm{FL} = 59.9\,(1 - e^{-0.168[t-0.189]}) \text{ (Payne et al. 1990).}$$

Fork length was then converted to weight using the relationship provided by Martin and Olver (1980) for Lake Opeongo lake trout from 1953 to 1965:

$$\mathrm{Log}_{10}\,(\text{weight}) = -2.17984 + 3.09839\,\mathrm{Log}_{10}\,(\mathrm{FL})$$

Weight was calculated for each age group annually, and used to derive total biomass values for fish ≥6 yr.

A constant of 1.6 eggs g^{-1} (Martin and Olver 1980) of adult female lake trout (age 6 yr and older) was used to determine total annual egg production. It was assumed that all adult females (≥6 yr) spawn every year, and that the sex ratio of male and female adult fish was 1:1. Payne et al. (1990) reported age specific maturity curves for Ontario lake trout, indicating only 10–20% maturity at age 6 yr and full maturity at 9–11 yr. The earlier age of maturity adopted here would be expected to make our simulated population more resistant to fishing and stocking than later maturing stocks. Mortality from egg to age 1 yr incorporated all losses from body cavity egg to the yearling stage.

Model Simulations

The model was tested for its ability to simulate the approximate equilibrium structure of the present Lake Opeongo population (Shuter et al. 1987). The model successfully simulated the "observed" structure of the Opeongo population and attained stability over 100 yr at the presently observed levels of natural and fishing mortalities of the adult trout. This was

taken as evidence that the model was performing satisfactorily. Further evidence of the general robustness of the model was its ability to attain equilibrium when fishing mortality was eliminated. The predicted equilibrium structure of the unexploited population was similar to that expected (Power 1978), with fewer young fish and increased abundance of large, old fish.

The basic simulation sets run on the model were as follows:

Simulation set	Conditions
A	No stocking, survival of wild eggs (S_{wo}) at 0.004 and varied F from 0–1.8
B	No stocking, varied S_{wo} from 0.0005–0.005, varied F from 0–1.8
C	Stocking at 5 yearlings ha^{-1}, S_{wo} = 0.004 or 0.002, varied F from 0–1.8
D	Varied stocking from 1–5 yearlings ha^{-1}, S_{wo} = 0.004, held F at 0.8

Simulation set A explores the effect of fishing at constant egg to yearling survival, while set B explores the effects of variation in egg to yearling survival and fishing mortality. Simulation sets C and D describe the combined effects of stocking and fishing on the abundance of wild and hatchery lake trout. Under each set of early survival and fishing mortality conditions, we compiled the number of 1-yr-olds, 4-yr-olds, total population size (age 1–20 yr), and the number of adult lake trout age 6 yr and older during each year of the simulation. Each simulation was run for 100 yr. The population structure under each set of mortality conditions was characterized by calculating the average number of fish within each year-class for the final 25 yr of each simulation (i.e. years 76–100).

We explored the effect of stocking of hatchery-reared yearling lake trout on adult (age 6–20 yr) population size, and the contribution of hatchery trout under various reproductive and juvenile survival scenarios (simulation set C). Survival of the stocked juvenile trout and their subsequent reproductive success was varied as follows: (1) juvenile survival of the hatchery trout equal to the wild trout, with normal reproductive success of the wild trout, but no natural reproduction of hatchery trout; (2) juvenile survival of the hatchery trout equal to that of the wild trout, and reproductive success of the hatchery trout either equal to or one half that of the wild trout; (3) juvenile survival of the stocked trout one half that of the wild trout with normal reproductive success of the wild fish, but no natural reproduction of the hatchery trout; (4) juvenile survival of the stocked trout one half that of the wild trout and reproductive success, either equal to or one half that of the wild fish. Reproductive success of the wild fish was set at two levels: one (S_{wo} = 0.004) representing strong early survival expected in a pristine environment provided nearly ideal conditions for the performance of wild fish in the presence of stocked hatchery-reared lake trout; the second (S_{wo} = 0.002), representing relatively low early survival was possibly more typical of lakes receiving supplementation stocking.

In a final set of simulations (simulation set D), we assessed the effects of varying the annual stocking rate (1, 3 and 5 yearlings ha^{-1}) at a fixed and relatively high level of instantaneous fishing mortality (F = 0.8). The same four juvenile survival and reproductive scenarios were simulated as in simulation set C.

Case History Studies of Lake Trout Stocking in Ontario

Long-term records of lake trout stocking in two Ontario lakes were compared to the predictions of our population model. The first record is for Lake Simcoe, a 725 km^2 mesotrophic lake inhabited by cold, cool and warmwater fishes (Evans and Waring 1987). The lake is subject to several anthropogenic influences that might be operating on the lake trout population, including nutrient and silt loading, introduction of rainbow smelt, *Osmerus mordax*, angling exploitation, littoral zone habitat modification, and possibly chemical contamination from agricultural, manufacturing, domestic sewage, and atmospheric sources (Evans et al. 1988). All of these factors would be expected to lower the reproductive success of the lake trout population and accelerate the rate of displacement of the native stock by hatchery-reared lake trout. Fin-clipped yearling lake trout were first released into Lake Simcoe in 1966, and stocking has been continued annually to the present time.

The second case history involves Lake Manitou, a 108 km^2 lake located on Manitoulin Island in northern Lake Huron, where stocking began in 1952 with an initial release of fin-clipped yearling lake trout, followed by annual releases from 1958 to the present time. The only known significant anthropogenic influence on lake trout in Lake Manitou is angling exploitation, which contributes to a total annual mortality of approximately 50% of the adult lake trout stock (Henderson 1982). We employed our population model in two simulations, to predict the numbers of adult trout of wild and hatchery origin and the proportion of first-generation hatchery lake trout in the Lake Manitou population from 1952 to 1989. We entered the known stocking history and assumed an instantaneous natural mortality of 0.1, an instantaneous fishing mortality of 0.6 and a juvenile survival rate (age 1–3 yr) for the stocked fish that was 80% of the survival for the wild juveniles. Early survival (egg to yearling) for the wild trout was set at S_{wo} = 0.002. In one scenario, the hatchery trout did not reproduce, and in the second scenario, they were permitted to reproduce but at a lower rate of egg to yearling survival (S_{wo} = 0.001) than for the wild fish. Reproductive success of hatchery lake trout has generally been reported to be lower than for native lake trout (Krueger et al. 1986).

Stocking histories of one to two decades and corresponding contributions of hatchery lake trout were also reviewed for eight lakes in northeastern Ontario (Powell et al. 1986) and five lakes in southeastern Ontario (MacLean and Hooper 1981; Claytor et al. 1985).

Results

Model Sensitivity to Exploitation and Variable Early Survival

Interaction between early survival and fishing mortality (simulation sets A and B) had a major effect on the density-dependent, compensatory capacity of the population, as indicated by the number of 4-yr-old recruits (Fig. 1). When survival rates of the early life stages were high, the compensatory capacity was also high. As early survival was reduced, however, the level of fishing mortality (F) at which the compensatory capacity of the population was exceeded (i.e., the level at which new recruits begin to decline despite continued reduction in the number of adult cannibals) declined sharply from 1.0 at an annual early survival of 0.005 to near zero at 0.0005. Over the range of early survival (egg to yearling stage) that appears to be typical of Lake Opeongo lake trout

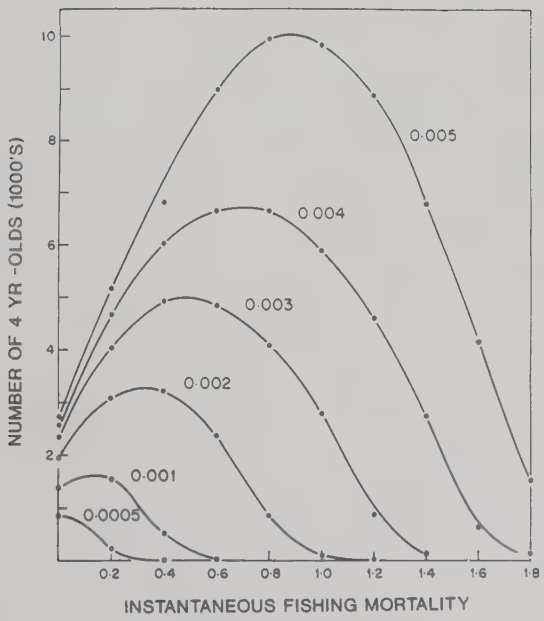

FIG. 1. The number of 4-yr-old recruits entering a hypothetical lake trout population in a 6 000 ha lake under various combinations of fishing intensities and egg to yearling survival rates.

(i.e. 0.002–0.003), the compensation capacity was exceeded when F reached 0.4–0.6 (Fig. 1).

Variable Fishing Mortality at Fixed Stocking Rate

High early survival

The effect of annual stocking at a fixed rate (simulation set C) on a self-sustaining lake trout population having strong early survival (S_{wo} = 0.004) is shown in Fig. 2a. Simulations were run at fishing mortalities from F = 0 to F = 1.8, at increments of F = 0.2. Figure 2a, curve A, indicates the predicted decline in adult population size as fishing mortality increased in the absence of stocking. When yearling lake trout were stocked (5·ha^{-1}·yr^{-1}) and their survival as juveniles (S_{hj}) was identical to the wild juveniles, and reproduction of the hatchery trout was set at zero (R_h = 0), the predicted total population size was significantly enhanced, especially at high fishing mortality (Fig. 2a, curve B). Under this circumstance, however, most of the population consisted of first-generation hatchery fish, the wild component of the population having been effectively replaced (Fig. 2a, curve C). The shaded area indicates the magnitude of the loss of wild fish that occurred simply as a result of numerical displacement of the wild fish by the hatchery fish. Even at F = 0.6 and a total annual mortality rate of 50%, the loss of wild adults exceeded 90%. At this level of mortality, a sizeable wild stock was able to persist in the absence of stocking (curve A). The small gain in population size (about 12%) achieved by stocking, therefore, resulted in a 90% loss of the wild stock.

When the hatchery fish did not reproduce (R_h = 0), and juvenile survival was low (S_{hj} = 0.5), there was only a very slight enhancement of the total population size at very high fishing mortalities, exceeding F = 0.8 (Fig. 2b, curve B). Loss of the wild component of the population was also greatly reduced under this scenario (Fig. 2b, curve C). The contribution of the hatchery fish to the population was dramatically reduced by poor juvenile survival. Under this circumstance, the

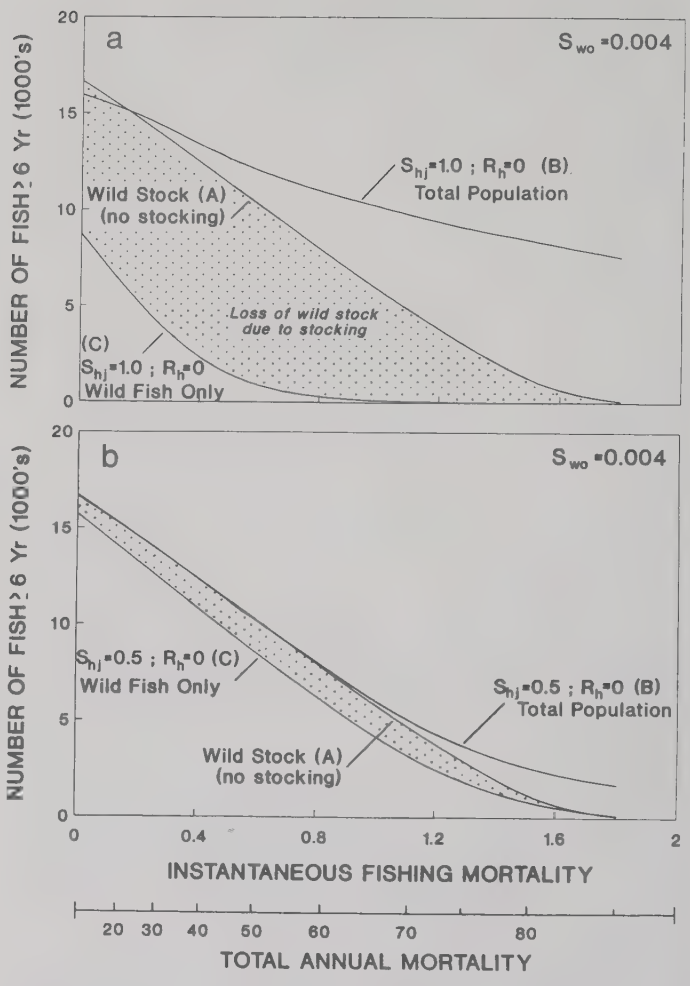

FIG. 2. *Panel a*: The number of adult lake trout in a hypothetical population in a 6 000 ha lake under various levels of fishing mortality in the absence (curve A) and presence (curves B and C) of stocked yearling lake trout, when egg to yearling survival is high (S_{wo} = 0.004) and survival of the hatchery juveniles is high (S_{hj} = 1.0). Stocking scenarios include the annual release of 30 000 yearlings (5 ha^{-1}) in each case. Reproduction of the hatchery trout was equal to zero (R_h = 0). The shaded area represents the loss of wild trout due to the combined effects of exploitation and stocking (5 yearlings·ha^{-1}·yr^{-1}). Each curve represents 10 simulations of 100 yr each. *Panel b*: The number of adult lake trout in a hypothetical population in a 6 000 ha lake under various levels of fishing mortality in the absence (curve A) and presence (curves B and C) of stocked yearling lake trout, when egg to yearling survival is high (S_{wo} = 0.004) and survival of the hatchery juveniles is low (S_{hj} = 0.5). Details are otherwise the same as in Panel a.

native stock continued to comprise a major component of the population, even at high rates of fishing mortality.

Low early survival

The effect of stocking on self-sustaining wild stocks of lake trout was even more dramatic when natural reproduction (i.e. survival from egg to yearling) was weak (S_{wo} = 0.002). In this situation (Fig. 3a), there was a significant enhancement of total adult population size, compared to the unstocked population (Fig. 3a, curve A), when S_{hj} = 1.0 and R_h = 0 (Fig. 3a, curve B), but the wild fish were completely replaced by the hatchery fish even when fishing and total annual mortality rates were very low (Fig. 3a, curve C). Comparison of the shaded areas in Fig. 2a and 3a indicates that weakly reproducing wild stocks

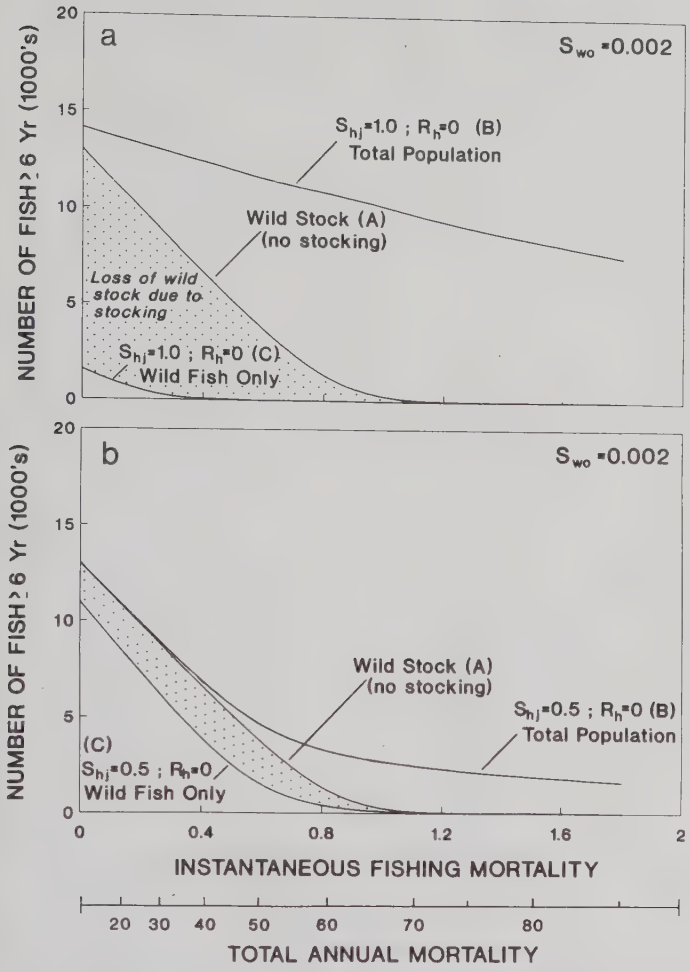

FIG. 3. *Panel a*: The number of adult lake trout in a hypothetical population of lake trout in a 6 000 ha lake under various levels of fishing mortality in the absence (curve A) and presence (curves B, and C) of stocked yearling lake trout, when egg to yearling survival is low (S_{wo} = 0.002) and survival of the hatchery juveniles is high (S_{hj} = 1.0). Details are otherwise the same as in Fig. 2. *Panel b*: The number of adult lake trout in a hypothetical population in a 6 000 ha lake under various levels of fishing intensity in the absence (curve A) and presence (curves B and C) of stocked yearling lake trout, when egg to yearling survival is low (S_{wo} = 0.002) and survival of the hatchery juveniles is also low (S_{hj} = 0.5). Details are otherwise the same as in Panel a.

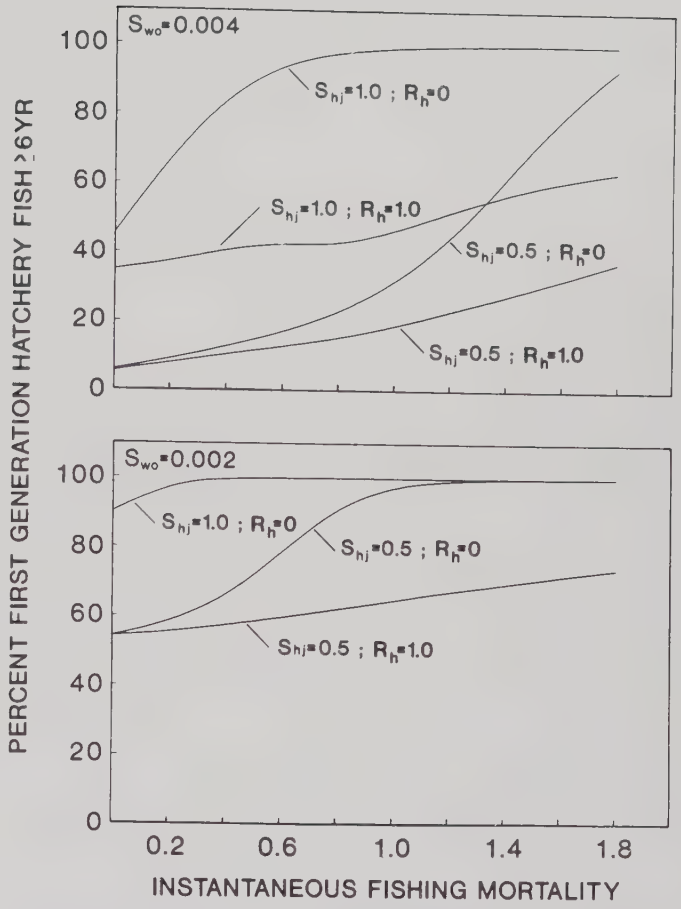

FIG. 4. Effects of various levels of fishing mortality on the percentage of hatchery lake trout in simulated stocked wild populations having either high (S_{wo} = 0.004, *upper panel*) or low (S_{wo} = 0.002, *lower panel*) egg to yearling survival. Juvenile-survival of the hatchery fish was either the same (S_{hj} = 1.0) or one half (S_{hj} = 0.5) that of the wild fish and their reproductive success was either zero (R_h = 0) or the same (R_h = 1.0) as the wild fish.

(Fig. 3a) have much lower resistance to displacement by hatchery stocks than strongly reproducing wild stocks (Fig. 2a). When juvenile survival was low (S_{hj} = 0.5) and reproduction of the stocked fish was zero, some enhancement over the unstocked population (Fig. 3b, curve A) occurred, but only at instantaneous fishing mortalities exceeding F = 0.4 (Fig. 3b, curve B). Again loss of wild stock indicated by the shaded area was much less dramatic when juvenile survival of the hatchery fish was low (Fig. 3b versus Fig. 3a).

The percentages of first-generation hatchery lake trout are shown in Fig. 4 for relatively strong (S_{wo} = 0.004) and weak (S_{wo} = 0.002) self-sustaining wild populations that had been stocked annually for 100 yr under various reproductive and juvenile survival scenarios for the hatchery fish. For simulations involving wild lake trout stocks with high early survival and good survival of hatchery juveniles (S_{hj} = 1.0), but no reproduction (R_h = 0) of stocked lake trout, we found that the wild stock was completely replaced at a fishing mortality of about F = 0.8 (Fig. 4, upper panel). In contrast, for wild populations having low early survival (S_{wo} = 0.002) and S_{hj} = 1.0 and R_h = 0 for the hatchery stock, the wild stock was lost at a fishing mortality of only F = 0.3 (Fig. 4, lower pond). For cases where juvenile survival of the hatchery fish was low (S_{hj} = 0.5) and reproduction was zero (R_h = 0), complete replacement of the wild stocks occurred at fishing mortalities of about F = 1.8 at S_{wo} = 0.004 and F = 1.2 at S_{wo} = 0.002, however, 50% replacement of the wild stock occurred at F = 1.3 and zero, respectively (Fig. 4). Scenarios in which the hatchery fish reproduced at the same rate as the wild fish (R_h = 1.0) resulted in much lower percentages of first-generation hatchery fish in the population. The higher percentage of natural progeny under these scenarios suggest the presence of wild fish but, in fact, the unmarked population would now be comprised primarily of the progeny of the hatchery fish.

Time Course of Population Loss Due to Stocking

The temporal pattern of replacement of exploited wild lake trout stocks by hatchery-reared lake trout stocks was similar for wild stocks having high and low early survival (natural reproduction), but loss of the wild stocks occurred at a much lower

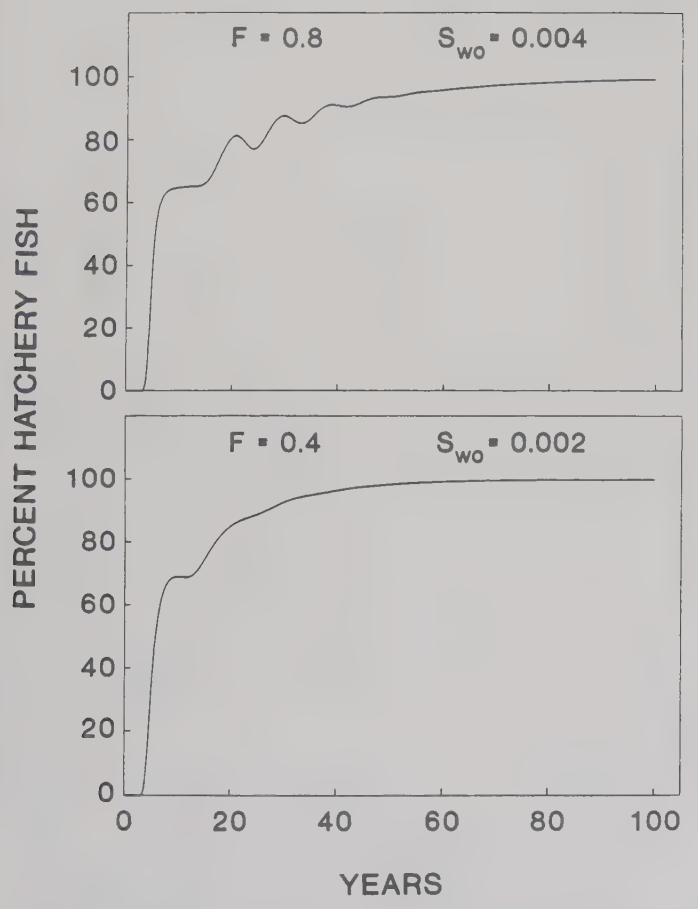

FIG. 5. Time course of changes in the percentage of hatchery lake trout in simulated, stocked populations having either high fishing mortality (F = 0.8) and high egg to yearling survival (S_{wo} = 0.004, *upper panel*) or moderate fishing mortality (F = 0.4) and low egg to yearling survival (S_{wo} = 0.002, *lower panel*). The stocking rate was 5 yearlings·ha^{-1}·yr^{-1}.

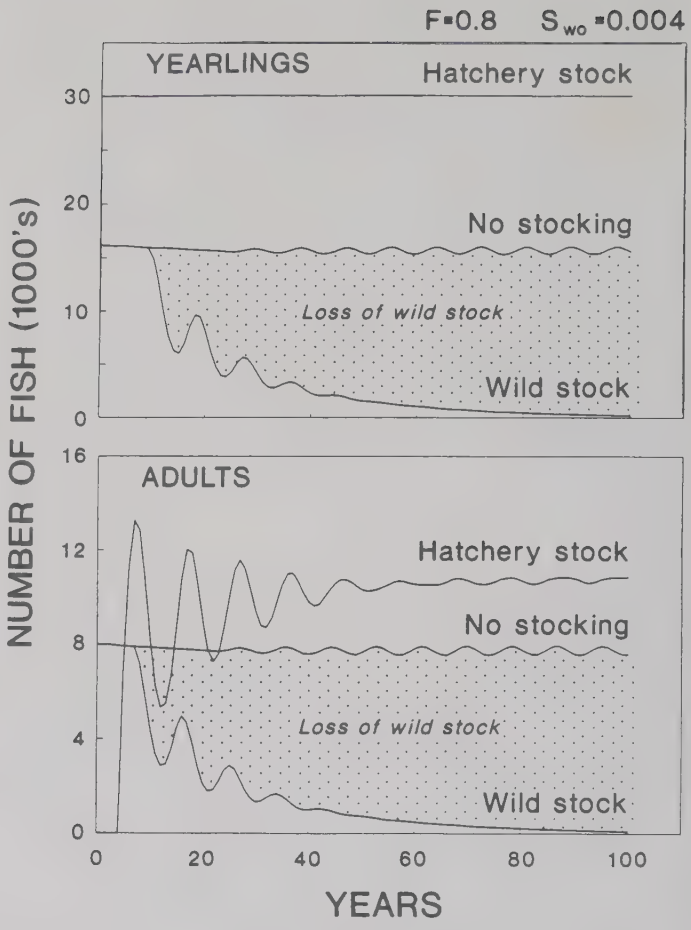

FIG. 6. Time course of the abundance of yearling (*upper panel*) and adult (*lower panel*) lake trout of wild and hatchery origin simulated at a constant stocking rate of 5 yearlings·ha^{-1}·yr^{-1} at high fishing mortality (F = 0.8) and high egg to yearling survival (S_{wo} = 0.004) of the wild fish. The shaded areas indicate the loss of wild yearlings and adults caused by the combined effects of high fishing mortality and displacement by the hatchery stock.

rate of fishing mortality for stocks having low recruitment rates (Fig. 5). Fishing rates causing 50% reduction of the unexploited stock in 100 yr simulations for stocks having high (Fig. 2) and low (Fig. 3) early survival were chosen for comparison. Under the two selected levels of natural reproduction (S_{wo} = 0.004 and 0.002), and fishing (F = 0.8 and 0.4, respectively), and with no reproduction of the hatchery lake trout, 80–90% of the adult trout in the modelled populations were comprised of first-generation hatchery fish after 20–30 yr of stocking at an annual stocking rate of 5 yearlings ha^{-1} (Fig. 5).

The actual numbers of yearlings and adults (6–20 yr) of wild and hatchery origin during the course of a 100 yr simulation for a strongly reproducing wild stock (S_{wo} = 0.004), subjected to an annual stocking rate of 5 yearling trout ha^{-1}, are shown in Fig. 6. The number of yearling trout of native origin is shown for a stable unstocked population and for a population under a constant stocking rate of 5 yearlings·ha^{-1}·yr^{-1} (upper panel). The loss of wild yearlings due to stocking is indicated by the shaded area in the upper panel. A similar plot is shown for the adults in the lower panel of Fig. 6. Oscillation of the adult hatchery stock is the result of year-class effects caused by density-dependent mortality of juveniles aged 1–3 yr. The number of wild yearlings simply tracked the number of wild adults. Loss of the wild stock occurred rapidly during the initial decade and progressed over several decades. Under this scenario, observations in the field, of variation in the numbers of wild adults, might give a false indication that natural recruitment was recovering between years 15 and 20, when the transient increase during these years actually represented an oscillatory feature of the downward trend in abundance (Fig. 6, lower panel). The adult age structures of the wild and hatchery stocks, including 4- and 5-yr-old recruits, clearly revealed the progressive loss of wild adults at decade intervals to year 40 (Fig. 7). Similar results were obtained for the weakly reproducing population (S_{wo} = 0.002), except at comparable fishing mortalities the loss of wild fish occurred more rapidly.

Effects of Variable Stocking Rates at Fixed Fishing Mortality

The effect of varying the stocking rate from 1 to 5 yearling lake trout·ha^{-1}·yr^{-1} was determined at constant mortality under a set of juvenile and reproductive scenarios for the hatchery fish (simulation set D). Under the mortality conditions in these simulations (S_{wo} = 0.004, F = 0.8, and M_2 = 0.1), the number of adult lake trout of native origin in the population in the absence of stocking was 7974 fish. The response to stocking was interpreted with reference to the unstocked population. The

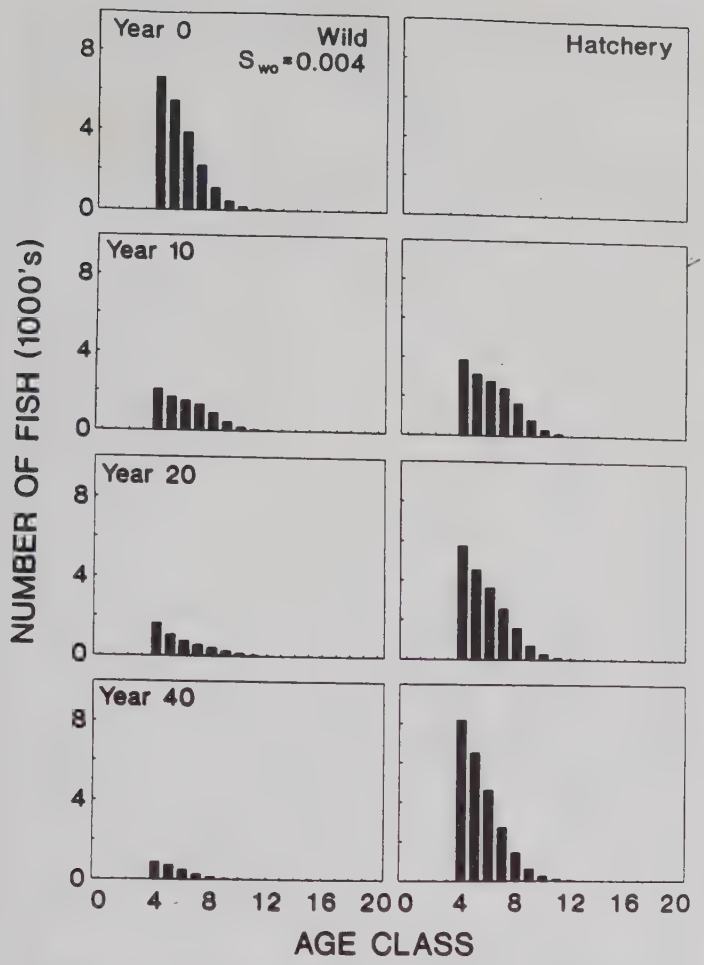

FIG. 7. Changes in age structures of simulated wild and hatchery stocks at decadal intervals at a stocking rate of 5 yearling lake trout·ha^{-1}·yr^{-1} under high fishing mortality (F = 0.8) and high egg to yearling survival (S_{wo} = 0.004) of the wild fish. The age structures are shown at intervals for the simulation illustrated in Fig. 6.

effects of stocking on the native population was strongly dependent on the stocking rate, and the juvenile survival and reproductive status of the hatchery fish (Table 1). For example, increase in the total population was 118% at a stocking rate of 5 ha^{-1}, but only 36% at a stocking rate of 1 ha^{-1} when juvenile survival and reproductive rate of the hatchery fish were equal to the wild stock. When juvenile survival (S_{hj}) was reduced to 0.5 and reproduction of the hatchery fish was zero, the increase in the total population was only 1 and 4% at stocking rates of 5 and 1 yearling ha^{-1}, respectively. Survival of the hatchery juveniles, in particular, had a major effect on their influence on the population. For example, at a stocking rate of 5 yearlings ha^{-1}, a 50% reduction in survival of the hatchery juveniles resulted in a decline from 118% enhancement of the population size to only 1%, as reproductive success of the hatchery fish declined from 1 to zero (Table 1). Reduction in juvenile survival resulted in markedly fewer hatchery fish in the population. At a low stocking rate of 1 ha^{-1}, a reduction in juvenile survival (S_{hj}) from 1.0 to 0.5 actually resulted in an increase in the enhancement to the total population, when there was no reproduction by the hatchery fish, because there were fewer adults of hatchery origin preying on natural recruits. The percentage of first-generation (clipped) hatchery adults also declined dramatically when juvenile survival declined by 50%.

At the commonly employed stocking rate of 5 yearlings·ha^{-1}·yr^{-1} and a juvenile survival rate of 0.5, the model predicted an enhancement of only 1–25% at a fishing mortality of F = 0.8, suggesting that stocking provides relatively low returns when natural recruitment is strong (S_{wo} = 0.004).

Lake Trout Stocking Histories

Lake Simcoe

The first stocking of fin-clipped, yearling lake trout in Lake Simcoe was in 1966, although lake trout fry and fingerlings had been stocked since 1880 (MacCrimmon and Skobe 1970). The contribution of the early fry and fingerling plantings is unknown, but is thought to be relatively small. Recent changes in abundance of fin-clipped, hatchery-reared lake trout reveals the build-up of the verifiable hatchery fish. The stocking history for fin-clipped, hatchery-reared, yearling lake trout, and the percent composition of hatchery adults captured in index trap nets during the fall spawning run, is shown in Fig. 8. Percent composition of fin-clipped lake trout increased from first occurrence (two fish) in 1969 to more than 90% by 1980, and by 1990 exceeded 99%. Thus in two decades, the unmarked population had been replaced by a free-ranging stock of hatchery origin, with little evidence of natural reproduction in recent years. The rapid transformation of the population suggests that earlier recruitment, whether from natural reproduction or stocking of unmarked fry and fingerlings, was relatively weak prior to initiation of yearling stocking in 1966. In general, the time scale for transformation of the population is consistent with the expected first occurrence of hatchery fish in the spawning run 4 yr after initial stocking (MacLean et al. 1981), and with predictions of our model, even though the reproductive status of the native component of the population was uncertain at the time of initial stocking of marked yearlings.

Lake Manitou

The 38 yr stocking history for Lake Manitou (Fig. 9) reveals an increasing level of stocking from 1952 to 1968, and a variable rate thereafter of 40 000–60 000 yearlings yr^{-1} (4–6 fish·ha^{-1}·yr^{-1}). The proportion of adult lake trout of hatchery origin on two spawning shoals in Lake Manitou tracks the stocking history (Fig. 9, lower panel). In the absence of actual data, proportions shown for 1956 and 1957 are estimates based on the average known age composition of the spawning population and expected time of appearance of fish from the 1952 stocking (Henderson 1982). Two major declines in the proportion of hatchery fish centered at years 1965 and 1972–73 appear to correspond to decreased stocking rates in 1960 and 1965, with lags of approximately one generation time. From 1973 to 1977, the proportion of hatchery fish in the spawning population increased from about 50% to 90%, and has varied from 85 to 98% from 1977 to the present (G. A. Clark, OMNR, Blue Jay Creek Hatchery, Manitoulin Island, Ont., pers. commun.). The pattern of change in the composition of the lake trout population following stocking is generally consistent with predictions of our model under a scenario of relatively weak natural reproduction of the native trout, moderate fishing mortality, and little or no reproduction by the hatchery fish. These conditions appear to be representative of the actual situation in Lake Manitou (Budd et al. 1986; Walker 1979; Henderson 1982).

Simulation of the Lake Manitou stocking history, using rough estimates for early survival (S_{wo} = 0.002), instantaneous fishing mortality (F = 0.6), and juvenile survival of the hatchery

TABLE 1. Summary of the effects of varying stocking rates of hatchery-reared yearling lake trout on the standing stocks of wild lake trout, first-generation hatchery lake trout and natural progeny under various levels of juvenile survival and various reproductive scenarios for the hatchery trout. The number of yearlings stocked corresponds to 5 ha $^{-1}$ (30 000), 3 ha $^{-1}$ (18 000) and 1 ha $^{-1}$ (6 000). Survival of the stocked juveniles ages 1, 2 and 3 yr (S_{h_j}) is indicated as a fraction of the survival of the wild juveniles (S_{wj}), which is determined as a function of adult biomass. Reproductive rate of the first-generation hatchery trout (R_h) is also given as a fraction of the reproductive success of the wild fish (S_{wo}), which was fixed at 0.004 for egg to yearling survival. Natural progeny includes pure wild stock and the progeny of first-generation hatchery trout. Mean number of fish (±SD) is shown for years 75–100 for each set of conditions. Fishing mortality was set at $F = 0.8$ for all simulations.

No. of yearlings stocked	Survival of stocked juveniles	Reproduction of stocked trout	Wild-unclipped fish			First generation hatchery			
				No. of fish >6 yr		No. of fish >6 yr		% of fish fin-clipped	Population enhancement numbers %
			Status	Mean	±SD	Mean	±SD		
0			Native stock	7974	1673				
30 000 (5 ha^{-1})	1.0	1.0	Natural progeny	10052	6854	7303	3914	42	118
		0.5	Natural progeny	5651	1936	8168	1817	59	73
		0	Native stock	248	73	10720	102	98	38
	0.5	1.0	Natural progeny	8475	2767	1520	255	15	25
		0.5	Natural progeny	7490	1954	1630	196	18	14
		0	Native stock	6234	1313	1799	147	22	1
18 000 (3 ha^{-1})	1.0	1.0	Natural progeny	9257	4384	5294	1730	36	82
		0.5	Natural progeny	6134	1196	5924	643	49	51
		0	Native stock	1241	156	7774	75	86	13
	0.5	1.0	Natural progeny	8392	2672	959	153	10	17
		0.5	Natural progeny	7770	2193	1013	134	12	10
		0	Native stock	7043	1801	1075	116	13	2
6 000 (1 ha^{-1})	1.0	1.0	Natural progeny	8610	3001	2267	423	21	36
		0.5	Natural progeny	7175	1717	2483	284	26	21
		0	Native stock	5096	785	2889	154	36	0
	0.5	1.0	Natural progeny	8330	2668	342	53	4	9
		0.5	Natural progeny	8096	2483	350	49	4	6
		0	Native stock	7901	2397	355	48	4	4

fish ($S_{hj} = 0.8$), and assuming no reproductive contribution of the hatchery fish, resulted in an irregular pattern of increase in the number of adult trout of hatchery origin and a corresponding gradual decline in wild lake trout (Fig. 10, upper panel). The predicted pattern of change in percent composition of hatchery fish closely parallels the actual change in composition of the spawning population (Fig. 10, lower panel), with the exception of a major negative deviation in the observed percent hatchery fish from 1971 to 1973. The cause of this deviation is not known, but appears to correspond with larger than average year-classes of unmarked lake trout for the years 1967 to 1969 (Fig. 6 in Henderson 1982). Another possibly confounding factor is that the quality of the hatchery fish was not necessarily constant over all years, even though the model assumes this to be so. Nevertheless, the predicted composition of the population is similar to the observed structure, suggesting that the wild lake trout stock in Lake Manitou has been displaced by the hatchery stock, as was the case in our earlier simulations of a hypothetical population.

Comparison of the catch-per-unit-effort (CUE) of stocked and native (unmarked) lake trout on spawning shoals in Lake Manitou, from 1959 to 1983, indicates marked increase in the total lake trout population as a result of stocking (Fig. 11). The catch of unmarked fish, however, has not declined as predicted in Fig. 10. Natural recruitment has remained relatively low, with the exception of two peaks centered at years 1965 and 1973, despite the build up of hatchery trout in the adult population. The relative contribution of hatchery versus native stock to natural recruitment is now impossible to determine given that native parental stock was used for hatchery production.

Several possible causes are suggested for the low level of recruitment at high spawning stock density: density-dependent suppression of natural recruitment by the stocked fish; environmental constraints on the natural production of lake trout, possibly habitat limitations for young-of-the-year trout; or low reproductive success of the hatchery-reared trout and suppression of reproductive success of the reproductively-viable wild component of the population through a combination of the effects of fishing mortality of adults and density-dependent suppression of juvenile survival. Increase of the hatchery stock independently of changes in recruitment of the wild (unmarked) stock suggests that agreement between the observed and predicted percent hatchery fish (Fig. 10) might be coincidental rather than explicative. Increase in the percentage of hatchery fish might simply reflect the increased abundance of hatchery fish rather than a substitution of the wild stock. Alternatively, a low level of reproduction of the hatchery stock might also generate a stock composition similar to that predicted by our model, the natural recruits being progeny of hatchery-reared parents rather than wild, native parents. A second simulation, in which reproduction of the hatchery fish was permitted, but

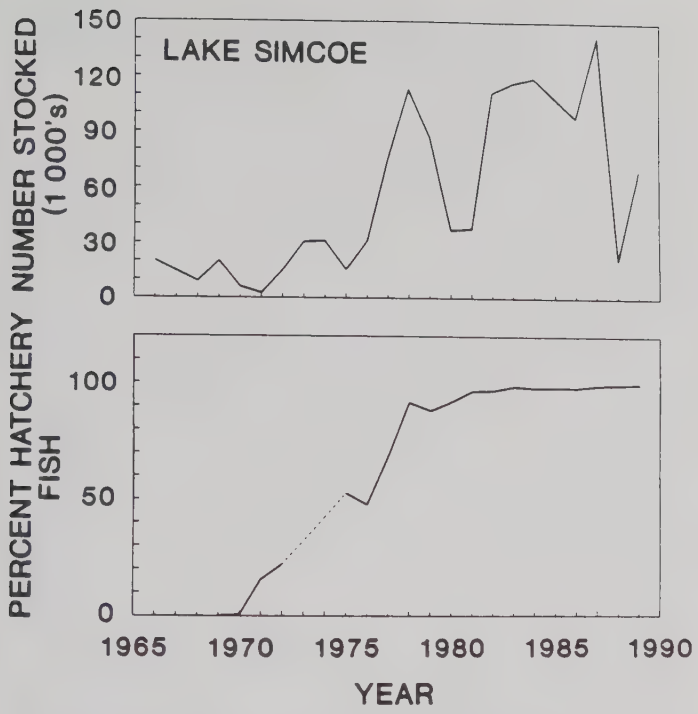

FIG. 8. Stocking history of yearling lake trout (*upper panel*) and percentage fin-clipped hatchery fish (*lower panel*) in the lake trout population of Lake Simcoe, 1966 to 1989.

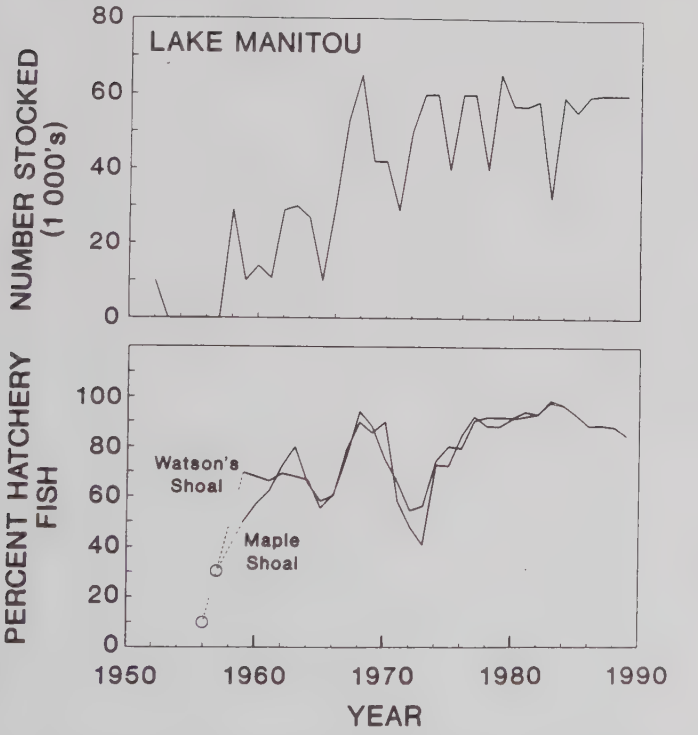

FIG. 9. Stocking history of yearling lake trout (*upper panel*) and percentage of fin-clipped hatchery fish (*lower panel*) in the spawning lake trout population of Lake Manitou, Ontario, 1952 to 1989. The catch data is uncorrected for multiple recaptures within years.

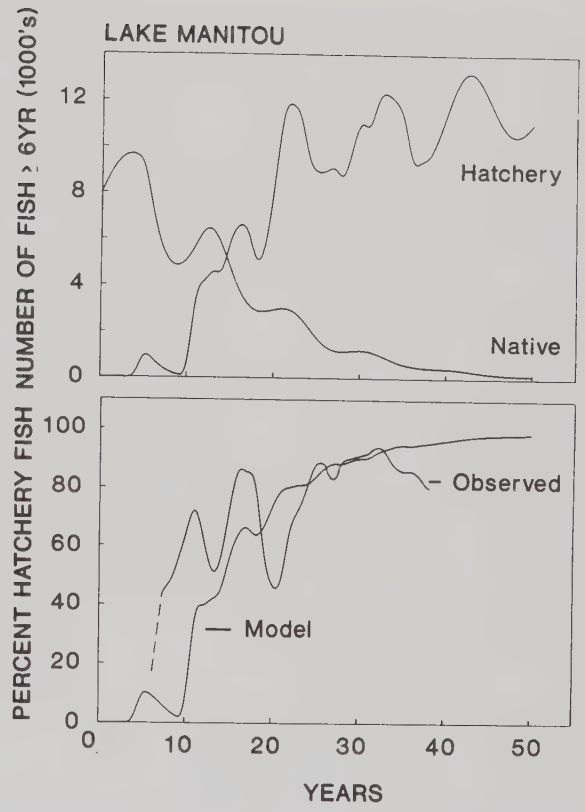

FIG. 10. Simulated changes in the number of adult lake trout of wild and hatchery origin in Lake Manitou, Ontario, using the actual stocking rate from 1952 (year zero) to 1989 (see Fig. 9) and continuing from 1989 to year 50 at a stocking rate of $6 \cdot ha^{-1} \cdot yr^{-1}$. In this simulation, the hatchery fish did not reproduce, fishing mortality was set at $F = 0.6$, and egg to yearling survival of the wild fish (S_{wo}) at 0.002. The lower panel shows the simulated and observed percent hatchery (fin-clipped) lake trout in the Lake Manitou population.

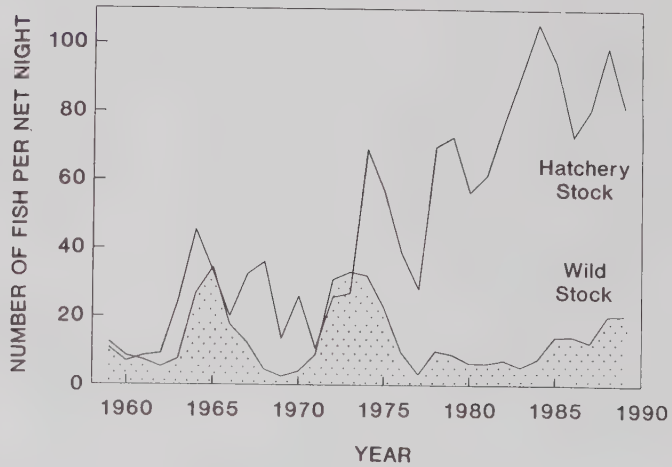

FIG. 11. Actual changes in the CUE of spawning adult lake trout of wild and hatchery (fin-clipped) origin in Lake Manitou, Ontario from 1959 to 1989. The catch data were corrected for multiple recaptures within years, based on the incidence of recoveries of tagged trout over the years 1958 to 1961, inclusive.

at a lower rate (S_{no} = 0.001) than the wild fish (S_{wo} = 0.002), resulted in a pattern of abundance of hatchery (fin-clipped) and wild (unmarked) adults that more closely fitted the observed pattern (Fig. 12). This scenario suggests that the wild unclipped population is now primarily comprised of the progeny of hatchery stock that have displaced the wild stock.

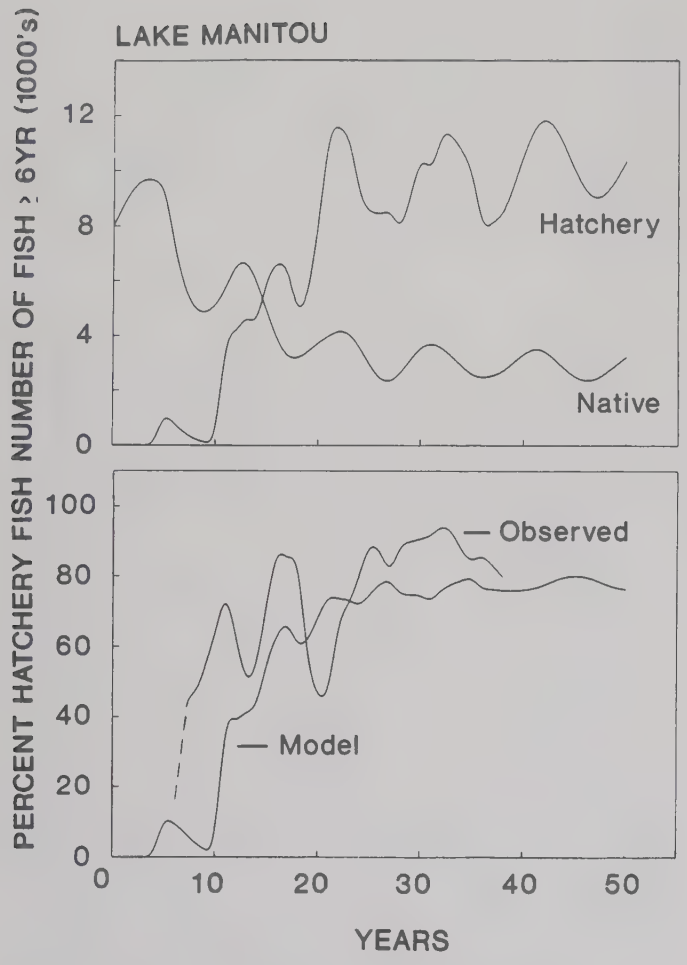

FIG. 12. Simulated changes in the number of adult lake trout of wild and hatchery origin in Lake Manitou, Ontario, as in Fig. 10, except that the hatchery fish were allowed to reproduce with egg to yearling survival set at $S_{ho} = 0.001$

Other case studies

Several other case studies of lake trout stocking on self-sustaining native stocks provide additional information on the interaction of hatchery and wild stocks (Table 2). In general, hatchery stocks are most successful when natural reproduction of the wild stock is poor and vice versa. This is best shown for North Anvil, South Anvil, Shakwa and Rushbrook lakes among those having weak natural reproduction, and Net and Devil lakes among those having strong natural reproduction (Table 2). Lakes Manitou and Simcoe also fall into the category of weak, natural reproduction. These observed outcomes are generally consistent with the predictions of our model, which revealed extreme sensitivity to stocking for wild lake trout populations having relatively weak, natural reproduction, or reduced densities due to high exploitation rates.

Discussion

Simulation modelling generally supported our two main hypotheses: (1) that stocking of hatchery-reared lake trout results in the loss of native stocks; and (2) that high fishing mortality accelerates the rate of displacement of native stocks by hatchery stocks. Notably, our simulations revealed that even in the absence of reproduction of introduced stocks or interbreeding of introduced stocks and native stocks, stocking of hatchery-reared lake trout can lead to the loss of the native gene pool. Within the assumptions and constraints of our model, there are three primary causes for the displacement of wild stocks: (1) when artificial recruitment exceeds natural recruitment, wild stocks are simply numerically outnumbered; (2) at hight rates of fishing, large mature adults are removed, thereby lowering the reproductive potential of the population, this is especially damaging to wild stocks that depend on natural recruitment and generally recruit at much lower rates than hatchery supported stocks (Wright 1981; Argue et al. 1983; Reisenbichler and McIntyre 1986); and (3) a large population of non-reproducing adult trout of hatchery origin will continue to cannibalize the wild juveniles, even though wild adults and juveniles are at low density. Two additional possible behavioural interactions between wild and hatchery stocks are of potential importance, although neither one has been substantiated nor incorporated within the model. These are spawning interference between wild and hatchery trout, and predation or exploitative competition by hatchery yearlings on wild alevins when the latter emerge from the incubation habitat and migrate to deeper water during spring.

We conclude that there is a synergism between the effects of stocking and fishing exploitation that accelerates the effects of introduced stocks on native stocks of lake trout. High exploitation rates, especially in small lakes, cause stock depletion leading to the initiation of stocking (Evans et al. 1991b). Stocking, in turn, stimulates fishing, or at least sustains fishing pressure at rates in excess of the capacity of the natural production system to provide new lake trout recruits. In an extreme case, exploitation could theoretically remove all mature adults, thereby preventing any natural reproduction and resulting in the loss of the native stock within one generation. This would be unlikely to happen in the absence of stocking, because fishing effort would decline as the catch rate becomes lower, and eventually most anglers would move to another lake, which would allow the stock an opportunity to recover. It is possible, however, that less mobile angling populations might inflict greater depredations on local stocks.

Stocking can sustain high fishing pressure and catches under intensive exploitation (Evans et al. 1991b), but the high mortality rates that this causes are bourne by both the hatchery and native stocks (Larkin 1974; Argue et al. 1983). According to our model, the actual effect depends on the reproductive status of the native and hatchery stocks, wild stocks having strong natural reproduction being more resistant to displacement. Stocking often results in little or no contribution of hatchery fish to the recipient population (Table 2). Purych (1977) and Powell et al. (1986) concluded that stocking on strong, self-sustaining wild stocks was ineffective. Stocked yearling lake trout are known to be highly vulnerable to cannibalism (MacLean et al. 1981), which possibly explains their poor survival in the presence of viable wild stocks. The converse of this is that poorly recruiting wild stocks are most vulnerable to displacement by hatchery stocks. Less productive wild stocks are also the most prone to overexploitation and as a result are the first stocks to receive supplementation stocking. Our model simulated both of these types of outcomes. The model also predicted a dramatic loss of wild fish, due to stocking and high exploitation, even when reproduction of the hatchery fish was zero. When natural reproduction of hatchery fish does occur, the loss of wild fish is masked, because unmarked progeny of the hatchery fish are normally indistinguishable in the field from the wild native fish. Unfortunately, the fitness of naturally

TABLE 2. Summary of several case histories involving stocking of hatchery-reared lake trout on self-sustaining wild populations in Ontario.

Region of Ontario	Lake name	Lake area (ha)	Years of stocking yearling lake trout	Stocking rate (no ha^{-1})	Status of hatchery stock	Reproductive status		% hatchery fish in the population			Source
						Wild stock	Hatchery stock	Years	Mean	± SD	
Northeastern	Wawa	678	6	11.2	Non-native	Fair	Unknown	4	37	21	Powell et al. (1986)
	North Anvil	92	7	16.2	Non-native	Weak	Unknown	4	77	12	
	South Anvil	74	7	19.1	Non-native	Very weak	Unknown	4	80	14	
	Peshu	389	8	15.2	Non-native	Fair	Unknown	4	19	12	
	Mount	345	7	11.7	Non-native	Fair	Unknown	4	36	24	
	Shakwa	649	11	7.5	Non-native	Very weak	Unknown	4	88	7	
	Rushbrook	174	11	11.5	Non-native	Very weak	Unknown	4	69	47	
	Net	711	9	9.2	Non-native	Very strong	Unknown	3	1	2	
Southeastern	Big Clear	187	24	8.2	Non-native	Fair	Unknown	4	47	9	Claytor et al. (1985)
	Big Rideau	5761	24	2.2	Non-native	Fair	Unknown	4	63	8	
	Big Salmon	148	20	10.2	Non-native	Fair	Unknown	4	59	9	
	Charleston	2517	30	5.5	Non-native	Strong	Weak	4	57	8	MacLean and Hooper (1981)
	Devil	1062	27	3.7	Non-native	Strong	Weak	4	13	6	
Manitoulin Island	Manitou	10300	33	4.0	Native	Fair-weak	Unknown	31	78	14	Henderson (1982)
South Central	Simcoe	72500	25	0.8	Native	Weak	None	12	96	3	This study

recruited fish of hatchery parents would be expected to be lower than wild native stock.

Field studies suggest that non-native stocks are less fit than their wild native counterparts, even when the former are the progeny of free-ranging wild fish (Altukhov 1981). Hatchery-reared, non native lake trout stocks have been found to have lower viability than similarly reared native stocks (Plosila 1977; Maclean et al. 1981). Also, Ihssen et al. (1988) found that transplanted stocks of lake trout had less genetic variability than the donor stocks from which they originated. In related studies, Altukhov and Salmenkova (1988) reported a much lower rate of return to spawning streams by non-native stocks of chum salmon (*Oncorhynchus keta*), and suggested that the rate of return was inversely related to the genetic distance between the donor and native stocks. Domesticated hatchery stocks of non-native origin would be expected to be even less fit than transplanted wild stocks, because of genetic differences introduced by hatchery breeding and rearing practises (Fraser 1981). Loss of genetic variability and associated loss of fitness has, in fact, been well documented in hatchery stocks of salmonids (Allendorf and Leary 1988; Allendorf and Ryman 1988).

The results of our simulations depend on several assumptions within the model. Most importantly we assumed density-dependent mortality in juvenile lake trout due to cannibalism by adults. Data for Opeongo lake trout supports the existence of density-dependent recruitment (Matuszek et al. 1990; Payne et al. 1990), but juvenile mortality might not be restricted to cannibalism. We also explored an alternate stock-recruitment function in which survival from egg to yearling was dependent on adult biomass (age 6–20 yr). In that case, stocking had an even more dramatic displacement effect on the abundance of the wild stock, because the hatchery juveniles which entered the population as yearlings, were not subjected to the density-dependent mortality. We also assumed that the behaviour of wild and hatchery lake trout is similar, especially in terms of cannibalism by adults. There is some evidence to suggest that behavioural differences exist between hatchery and wild lake trout (Krueger et al. 1986), but whether their depth distributions and cannibalistic behaviours are different is unknown. The model does accommodate differential survival of the juveniles by allowing mortalities of the stocked juveniles to be independently modified. Finally, both stocked and wild lake trout were assumed to be equally vulnerable to the fishery. Deviations from any of these assumptions would be expected to cause some, possibly significant, changes in the results of our simulations.

Consideration of the potential breeding interactions between native and hatchery lake trout also raises a number of additional questions about the reproductive biology of wild and introduced lake trout stocks. For example, it is not known whether the introduced stocks segregate from the indigenous wild stocks during spawning, or whether they interbreed or attempt to interbreed with the native fish. MacLean et al. (1981) noted possible segregation of one introduced, non-native stock in Lake Simcoe, Ontario, during the breeding period. Similarly, spawning aggregations in Charleston Lake and Devil Lake, Ontario, were primarily comprised of native fish, even though 50 and 17% of the fish in the non-spawning populations were of hatchery origin (MacLean and Hooper 1981). Electrophoretic analyses of these populations revealed little or no evidence of reproductive contribution of non-native trout to the unmarked (wild) component of the population, even though yearling lake trout of non-native origin had been stocked annually in both lakes for about 25 yr (P.E. Ihssen, OMNR, Maple, Ont. L6A 1S9). These results suggest that hatchery-reared lake trout in Charleston and Devil lakes do not reproduce successfully, either in hybrid or pure matings. In contrast, natural reproduction of the wild trout is strong in both lakes. Hatchery-reared lake trout are known to be capable of reproduction in the wild from studies of introductions to lakes not previously inhabited by lake trout (Hitchins and Samis 1986), but apparently in some cases do not reproduce successfully even when densities of hatchery trout are relatively high (e.g. Krueger et al. 1986).

If native and hatchery-reared lake trout were to interbreed freely, the risk of loss of the wild stock through introgressive hybridization (Ryman 1981) would have to be considered. Sterilization has been proposed as a solution to the problem of introgression of hatchery genes into wild gene pools (Donald-

son and Hunter 1982), although introgressive hybridization has not been reported for lake trout stocks. The results of our study, however, suggest that sterilization of stocked lake trout would not be an effective solution to the problem of wild stock displacement by hatchery stocks, especially under intensive fishing pressure.

By examining several long-term stocking case histories, we have attempted to question the validity of our simulation results. In general, the field evidence is consistent with predictions of the model, keeping in mind that our intension was to explore possible biological outcomes, not to provide precise predictions. The model, while omitting some possibly important features of lake trout population dynamics such as growth compensation, variability in maturation schedules, and winter fishing, is generally consistent with present understanding of the dynamics of piscivorous lake trout populations in Ontario lakes. In reality, however, the available data provides only some circumstantial consistency and certainly not proof of the proposed mechanisms. While the details of the responses to stocking must be considered tentative, we suggest that the generalities provide some important inferences about the interactions of wild and enhanced stocks of lake trout.

In summary, supplemental stocking of native lake trout populations with hatchery-reared lake trout stimulates angling and tends to maintain high fishing intensities and yields (Evans et al. 1991b). In some lakes, however, stocking has little effect because survival of the hatchery trout is low. Our model and the available field data sugest that the success of stocked lake trout is determined by the reproductive capacity of the recipient native stock and the level of exploitation, less productive wild stocks being most vulnerable to displacement by stocking. Cannibalism of stocked lake trout by wild lake trout (Martin and Olver 1980; MacLean et al. 1981) may explain the lack of success of stocked lake trout in lakes having viable wild stocks. Gunn et al. (1987) concluded that competition among juveniles played a role in the survival of successive plants of hatchery-reared lake trout in lakes having very few or no wild lake trout. In other lakes, high stocking rates (artificial recruitment) needed to sustain high rates of exploitation usually greatly exceed natural recruitment (Evans et al. 1991b). In such cases, our model predicts that wild native stocks are replaced by hatchery stocks, even when the latter do not reproduce. If the same or a few hatchery stocks are used widely for supplemental stocking of native populations, the effect would be to dramatically reduce genetic heterogeneity.

Stocking of hatchery-reared stocks is often conducted on a trial and error basis, success being measured simply in terms of survival of the stocked fish, usually to the anglers creel. Greatest stocking success is generally achieved when reproduction of the recipient stock is low, but rarely, if ever, are the risks of damage to the recipient wild stocks adequately considered. Unfortunately, the risk appear to be greatest when the recipient stocks are already weakend by exploitation, habitat degradation, or other stressors, the conditions under which stocking is most likely to be initiated. Our results identify the need for basic research on the biology of lake trout and on the interactions between wild and hatchery stocks, to adequately appraise the risks of stocking. Additional information is needed on spatial distribution, interactions between life stages (cannibalism), mortality schedules, reproductive biology, habitat requirements, and population genetics, to better understand the interactions between wild and hatchery stocks. In addition, our results have important implications within the broader context of policy development for management of lake trout and other species that might be similarly affected by enhancement activities. We recommend that emphasis be placed on protecting the genetic integrity of the remaining self-sustaining wild stocks and that a moratorium be considered on supplemental stocking of these populations with non-native stocks.

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Selective Diversification of Aquaculture Stocks: A Proposal for Economically Sustainable Genetic Conservation[1]

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The genetic diversity of aquaculture stocks can be maintained, and their genetic impact on wild stocks minimized, by breeding programmes that deliberately generate genetic diversity. Current animal breeding practices are likely to reduce the diversity of domestic stocks if they are extended to aquaculture. It is proposed that national breeding programmes for aquaculture should, instead, try to develop numerous breeds specially adapted to local environments and aquaculture systems. An economic model is presented of decision-making by individual farmers who, in choosing which breed to produce, determine the "fitness" of the breeds in a meta-population that includes all breeds. As long as strong genotype-environment interaction for production traits is maintained by artificial selection, the economic self-interest of farmers should ensure the stability of genetic polymorphisms among breeds. Genetic variation would be conserved (in the among-breed component of genetic diversity) but not the primordial distribution of gene and genotype frequencies. Economic benefits to farmers, plus a high return on investment at the national or supra-national level, makes breed diversification an attractive conservation strategy even though it is admittedly a compromise from a purely genetic viewpoint.

On peut maintenir la diversité génétique des stocks de poisson d'élevage et minimiser les conséquences de leurs interactions avec les stocks sauvages en concevant des programmes de reproduction qui conduisent délibérément à une grande diversité génétique. Les pratiques d'élevage actuelle conduiraient vraisemblablement à une réduction de la diversité des stocks si elles étaient appliquées à l'aquaculture. On propose au contraire que les programmes d'élevage piscicole essaient d'avoir de très nombreuses races adaptées aux conditions et aux systèmes locaux. On présente un modèle de prise de décision pour l'aquaculteur qui désire choisir la race qu'il veut élever et déterminer dans quelle mesure les races d'une métapopulation de toutes les races sont adaptées à ses conditions. Tant que l'on maintient une forte interaction génotype-environnement pour les traits de production par sélection artificielle, les intérêts économiques des aquaculteurs devraient garantir la stabilité des polymorphismes génétiques des races. La variation génétique (à l'intérieur de la race choisie) devrait être conservée, mais pas la répartition primordiale des fréquences des gènes et génotypes. Les avantages économiques pour les aquaculteurs, plus un rendement élevé des investissements au niveau national ou supranational, rendent la diversité des races une stratégie de conservation attrayante, même si ce n'est qu'un compromis du point de vue purement génétique.

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The stock-improvement activities of animal breeders have drastically reduced the gene pool diversity of domestic animals during this century (Alderson 1989; Oldfield 1989). Similar losses in aquaculture are likely to lead to problems in the future when the genetic diversity of cultivated stocks has become a major component of the total diversity of intensively cultivated species. The thesis of this paper is that diversity could be maintained, and the adaptive flexibility of surviving wild populations might be conserved or enhanced, by adopting a genetic improvement strategy for aquaculture that differs from the usual strategies of animal breeders. The strat-

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egy proposed here is the *active generation* of genetic diversity among newly domesticated stocks. Our suggestion is that national aquaculture breeding programmes should, from their outset, develop a large number of breeds specially adapted to local environmental conditions and farming systems. It will be shown below that a diversity-generating programme can be economically advantageous to the individual farmer, and therefore should complement, rather than oppose, the worldwide acceleration of aquaculture production.

The proposal to actively generate genetic diversity in a national breeding programme is by no means unprecedented. Land (1981) recognized the need to develop, not merely conserve, genetic flexibility in domestic animals and proposed that national breeding programmes should include selective diversification among their breeding objectives. Similar recommendations were made by Smith (1985) who examined the effect of unpredictable changes in consumer preference, economic conditions and husbandry techniques on the genetic improvement of farm animals. The conclusion of Smith's economic analysis was that the long term interest of the agriculture community would be best served by the development of many biologically divergent breeds — on the order of 50 — as a hedge against uncertainty. Fifty seems unrealistically high for aquaculture until one considers that in just one country, Thailand, there are more than 15 government fisheries stations that produce fish "seed," and that could easily undertake small-scale strain development programmes.

From the perspective of a geneticist, the key feature of a genetic improvement strategy that promotes diversification is the attitude of the breeder towards genotype–environment (GE) interaction. Genotype–environment interaction occurs when the relative performance of genotypes or breeds varies among environments (Falconer 1981). It is generally assumed that GE interaction is of little practical importance if it is too small to alter the relative ranking of genotypes (weak GE interaction) in different environments (Baker 1988; Gregorius and Namkoong 1986; Westcott 1986). Our proposal, however, is to generate and maintain *strong*, or rank-changing, GE interaction among aquaculture breeds specialized for various aquaculture systems, habitats and geographical locations. The objective is to develop a suite of breeds, each of which is superior to all other breeds in at least one environment that is commercially, sociologically or politically important. A genetic diversification policy for aquaculture thus differs substantially from the majority of breeding programmes involving farm animals.

Conventional Animal Breeding Programmes Lead to the Loss of Genetic Diversity

The usual policy of scientific animal breeders has been to increase the potential yield, or other desirable traits, of a herd as quickly as possible, and to modify both the genetics and the environment of the herd as much as is required to do so. The result has been a drastic reduction in the genetic diversity of domesticated animals (Oldfield 1989; Alderson 1989). Of the many examples of such losses given by Alderson, one is quoted here at length because of its direct relevance to the future development of aquaculture (Alderson 1989, p. 7):

> At the beginning of this century Norway possessed about twenty breeds of cattle. By 1959 only seven recognized breeds remained, with the NRF (Norsk Rodtfe) making up about 30% of the national herd. This herd was then chosen as the medium for implementing government breeding policies, and breeders were encouraged and advised to use NRF bulls. The result is that 98% of the cattle in Norway are now of NRF type. It is frightening to consider both the speed of this process and the overwhelming effect of an imposed policy with government support. In the 1960s a series of breeds were carried away in the torrent of amalgamation with the NRF – the Rodt Tronderfe in 1960, the Raukolle in 1961, the Dole in 1963, and the SVF (Sor og Vestlansfe) in 1968. Only two breeds have so far resisted total capitulation, but both are on the verge of extinction: the Telemark is a mountain breed noted for its longevity, hardiness and thriftiness: the Sidet Tronderfe is a polled breed found in northern Norway. In 1984 it was recommended that Nordic Gene Bank Committee should be formed, including all the Scandinavian countries, but it is doubtful that these breeds can be saved unless there is a swift and dramatic change in policy.

Alderson's example is important because Norway is a recognized leader in the application of modern breeding practices to aquaculture on a national scale. It is not surprising that the Norwegian breeding programme for Atlantic salmon undertaken by the Institute of Aquaculture Research (Akvaforsk), as described by Gjedrem et al. (1988), is following a course parallel to that of the Norwegian cattle industry. Dr. Gjedrem estimates that currently about 70% of the Atlantic salmon farmed in Norway come from the selected Akvaforsk breed (personal communication 1990).

The policy of programmes like that of Akvaforsk is to minimize or ignore GE interaction whenever it is "weak" and does not significantly hinder the response to selection. The selection ideal is a single, all-purpose breed that increases yield across the range of commercial environments. The centralized genetic programme of Akvaforsk is a widely respected model for the future development of an aquaculture broodstock industry based on conventional animal breeding practices.

A Diversification Programme for Aquaculture Genetic Improvement

Fisheries biologists and conservationists tend to distrust both the logic and the optimism of the animal breeders. They find themselves at a disadvantage, however, because their position is often seen as obstructive. It is easy to show that improved aquaculture stocks and increased aquaculture production are genuinely needed, and needed with increasing urgency, as natural fish stocks become exploited to the point of collapse (FAO 1989). This conflict between genetic conservation and commercial development in aquaculture again finds its parallel in animal husbandry (Alderson 1989, p. 105):

> The philosophy of genetic conservation . . . is based on the apparently negative concept of maintaining the status quo, and that is what is so difficult for many scientists and livestock breeders to understand. The idea is alien to the general tenets of livestock production, and conflict between the principle of conserving genetic variability and the instinctive urge to improve — or more accurately to change — is an accepted feature of the conservation of rare breeds.

To try to resolve this conflict we propose a *diversification* policy for aquaculture genetic improvement at the national level. In a later section we outline evidence that breeds generated in such programmes might change rapidly under selec-

tion for increased yield in their particular environments. The evolving ensemble of specialized breeds would constitute a reservoir of genetic diversity that more closely resembles the ancient "crop gene centres" (Oldfield 1989) than it does the untouchable genetic reservoir of a gene bank. (Crop gene centres are the geographically localized origins of primitive cultivars or breeds of domestic plants and animals.) Diversity would be conserved in these modern analogues to the crop gene centres, but not their "primitiveness," as the population would be under intense selection both within and between breeds. Selective diversification is a compromise between the need to reconcile the indisputable need for increased aquaculture production with the need for genetic conservation. Genetic variation is conserved, but not the status quo, ie. the primordial distribution of gene and genotype frequencies.

Considered as a group or "gene centre," the breeds should evolve towards the domesticated condition if there is occasional genetic interchange among them, by analogy with the predictions of Wright's shifting-balance theory for natural populations (Crow et al. 1990). The among-breed component of diversity in the domesticated "metapopulation" (Olivieri et al. 1990) should remain high both for neutral alleles and those affecting fitness. The breeds will not evolve towards genetic uniformity unless two conditions are met: (a) a single genotype becomes superior in all environments (Gillespie and Turelli 1989), and (b) all farmers select, ie choose to cultivate, that genotype. In our economic model (see below) farmers are assumed to select both within and among breeds on the basis of economic self-interest.

Maintenance of strong GE interaction in a diversification programme is the key to the success of the long-term conservation strategy. Genetic interchange (eg. escapes or deliberate hybridization) may produce breeds that do well in several environments. Hybridization may increase the overall rate of domestication of the aquaculture metapopulation, but should be associated with continuing selection aimed at maintaining strong GE interaction among the breeds. While strong GE interaction is maintained by artificial selection there is no tendency towards the homozygosity, or isogenicity, that has greatly increased the sensitivity of terrestrial crops and animals to disease, insects and climatic stress (Plucknett and Smith 1982; Alderson 1989) — and which is so worrisome to those concerned with the genetic impact of aquaculture.

Our proposed diversification strategy is clearly inconsistent with proposals to conserve genetic diversity by minimizing evolutionary changes in domesticated populations (Allendorf and Ryman 1987). Genetic conservation follows, instead, from the inherent stability of fitness polymorphisms that generate strong GE interactions in a heterogeneous environment (Gillespie and Turelli 1989). Fitness in the heterogeneous domestic environment depends on the willingness of farmers, firstly, to use breeds that are specialized for their particular environment, and secondly to maintain the environmental heterogeneity itself (i.e. the diversity of farming systems). This willingness will depend on the financial benefits an individual farmer can expect from using the specialized breeds.

Is the Attainment of Strong GE Interaction a Feasible Objective?

A genetic diversification programme would have as its objective the generation of strong GE interaction among breeds, whether or not such interaction is present in the founder breed or breeds. The biological properties of breeds will diverge under selection when fitness — i.e. commercial performance — involves different, but genetically correlated, heritable traits in contrasting environments. In general, the direct response of each breed to selection in its own environment will be greater than its correlated response in other environments, so selection in both environments (given sufficient genetic variance) will result in strong GE interaction — eventually. The rate of breed divergence will depend on the intensity of selection in each environment and the genetic variances and correlations of traits within and between environments (eg. Rosielle and Hamblin 1981).

Whether disruptive selection can in practice produce strong GE interaction in aquaculture is a question that can only be answered experimentally. The available evidence comes mostly from comparison between natural and aquaculture systems rather than between types of domestic environment. Breeds of fish adapted to high-input aquaculture tend to do less well than other breeds when tested in less intensively managed environments and *vice versa* (Fraser 1981; Doyle and Talbot 1986; Chilcote et al. 1986; Hjort and Achreck 1982). Genotype-environment interactions involving different types of domestic environment have been demonstrated in common carp (Wohlfarth et al. 1986) and catfish (Dunham et al. 1990). GE interaction between *C. carpio* breeds specialized for artisanal and intensive cultivation is well documented (Wohlfarth et al. 1986). There is growing evidence of GE interaction among tilapia breeds grown in the Philippines on high and low quality feeds (Romana and Doyle, unpubl. data) and on farms in Thailand (Uraiwan 1990). The environments in which fish are cultivated are at least as varied as those experienced by crop plants. In SE Asia, for example, they range from rain-fed rice fields, to manured ponds, to intensively managed ponds, cages and concrete raceways receiving pelleted feed (Brown 1983).

The adaptation of fish other than common carp (Wohlfarth et al. 1986) to the diversity of artifical environments is just beginning and represents a period of rapid evolution under intense environmental stress (Kohane and Parsons 1988). As in the case of domestic land animals (Price 1984), the domestication of fish is likely to involve feeding and social behaviour (Suboski and Templeton 1989). High intensity cultivation selects for less competitive and less reactive fish (Doyle and Talbot 1986), and increased tameness of domesticated stocks has already been noticed (Moyle 1969, Gjedrem et al. 1988). Behavioural requirements for successful foraging and predator avoidance will differ widely between intensively cultivated ponds and artisanal environments such as rice fields. It is clear that considerable variation exists in both the aquaculture environments and in the phenotypic response to these environments — i.e., there is considerable "opportunity for selection" (Downhower et al. 1987). We therefore suggest that strong GE interaction can probably be achieved when a natural population or primitive breed is selected in two or more dissimilar environments.

Example of a Genetic Improvement Programme Based on Diversification and Strong GE Interaction

A genetic stock improvement programme based on diversification would attempt to develop specialized breeds, probably through artificial selection. There is as yet no well-documented example of such a programme so we offer a purely hypothetical illustration (Fig. 1). In this illustration, selection carried out in

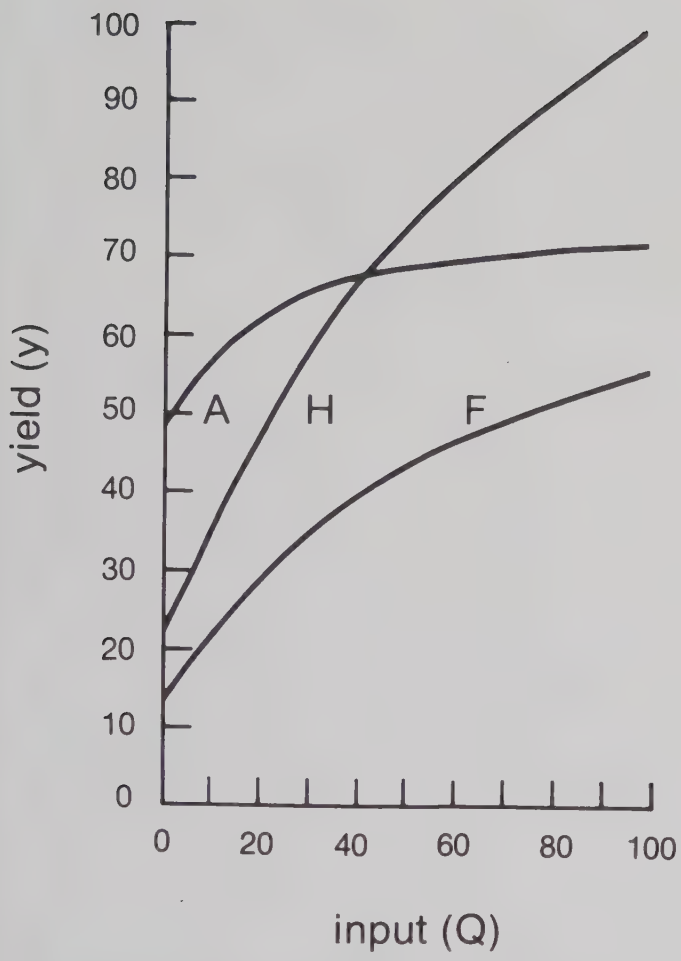

FIG. 1. Yields of specialized artisanal (A) and high-input (H) breeds generated by selecting a founder breed (F) in two aquaculture environments. The abscissa and ordinate are arbitrarily scaled to 100 units of input and yield, respectively.

low- and high-input environments has generated specialist breeds that rank differently at opposite environmental extremes (Moav et al. 1976). The environments in Fig. 1 are characterized by their "input" of feed, labour, electricity etc., and the breeds are characterized by their production functions, i.e. their characteristic yield in each environment. The hypothetical environments are differentiated on a scale of "input intensity" which can be interpreted in economic terms, rather than an environmental variable like temperature where economic parameterization would be more indirect and dependent on particular circumstances.

The hypothetical production function for the three breeds shown in Fig. 1, A (artisanal), H (high input) and F (founder) is

$$(1)\quad Y_i = \frac{1}{a_i + \dfrac{b_i}{g + Q_i}},$$

a rectangular hyperbola. The variable Y_i = yield of the i^{th} breed where i = A, H or F; the variable Q_i = variable inputs such as feed, "seed," electricity and labour. The parameter a_i measures (approximately) the energy accumulation rate of the i^{th} breed at saturating inputs, and b_i reflects assimilation efficiency at low inputs. The origin-translation parameter g represents fixed inputs common to both breeds that are not included in the model. The true form of production functions that relate the yield of aquaculture stocks to variable inputs of feed, labour, electricity etc. is unknown. We chose (1) for simulation because curves of this, or similar, mathematical form have proven useful for empirical analysis of many types of biological dose-response data (Ratkowsky 1983; Causton 1977).

Relationship Between Genetic Diversification, Economics and Social Development Policy

The early phase of the Green Revolution in field crops perfectly illustrates how modern breeding policies can reduce genetic diversity (in that case the diversity of crop cultivars). The newly developed, input-responsive varieties of wheat, maize and rice are sometimes said to yield as much as, or even somewhat more than, traditional cultivars under inferior conditions (Plucknett and Smith 1982) — typical weak GE interaction that has had enormous impact both on genetic diversity and human society despite being "weak." To achieve the high yields of which only the new varieties are capable, intensive cultivation has replaced traditional farming practices in many rural communities, often to the detriment of the poorer members of these communities (Castillo 1975). In reaction to the socioeconomic side effects of the Green Revolution, international crop research programmes are now developing varieties specialized for low inputs and marginal conditions (Oasa 1987). The surviving primitive cultivars constitute an important resource base for these genetic diversification programmes. There is now a growing concern that the genetic engineering of farm animals may renew the socioeconomic assault of modern genetics on small farms even in developed countries (Lesser 1990).

The distinguishing feature of the Green Revolution in field crop production has been synergy between the development of new varieties, increased use of fertilizers and pesticides, and rigorous monoculture. One might suppose that a similar course will be followed in aquaculture by programmes based on conventional animal breeding procedures if a single breed becomes increasingly adapted to (i.e., responsive to) technologically sophisticated management practices.

Assuming that the diversification simulated in Fig. 1 can be achieved, some of its socioeconomic consequences are explored in Fig. 2 and 3. To do this it is necessary to translate the biological differences among the breeds into economic terms. The analyses of Land (1981) and Smith (1985) dealt with the economic advantages of diversification for the farming community as a whole. We will be more concerned with the decisions of individual farmers, who in effect determine the fitness of the breeds and therefore the long-term stability of the genetic polymorphisms (assuming informed, free choice by the farmers).

Figure 2 shows the hypothetical net return (revenue − costs, or $Y_i - mQ_i$) achieved by farmers who grow the A, H and F breeds at constant costs and prices. The axes in this figure are scaled relative to the axes in Fig. 1 so that m, the cost/unit input, = cost/unit yield = 1.0. It is more profitable for an individual farmer to grow the artisanal breed at about 4 input units than either the H or the founder breed at any level of input. There is no financial incentive to switch from cultivation of the artisanal breed, within the range of Q shown here, despite the considerably higher yield of the latter under intensive cultivation. The relative net return from artisanal and high-intensity cultivation depends on the parameter values used in the model,

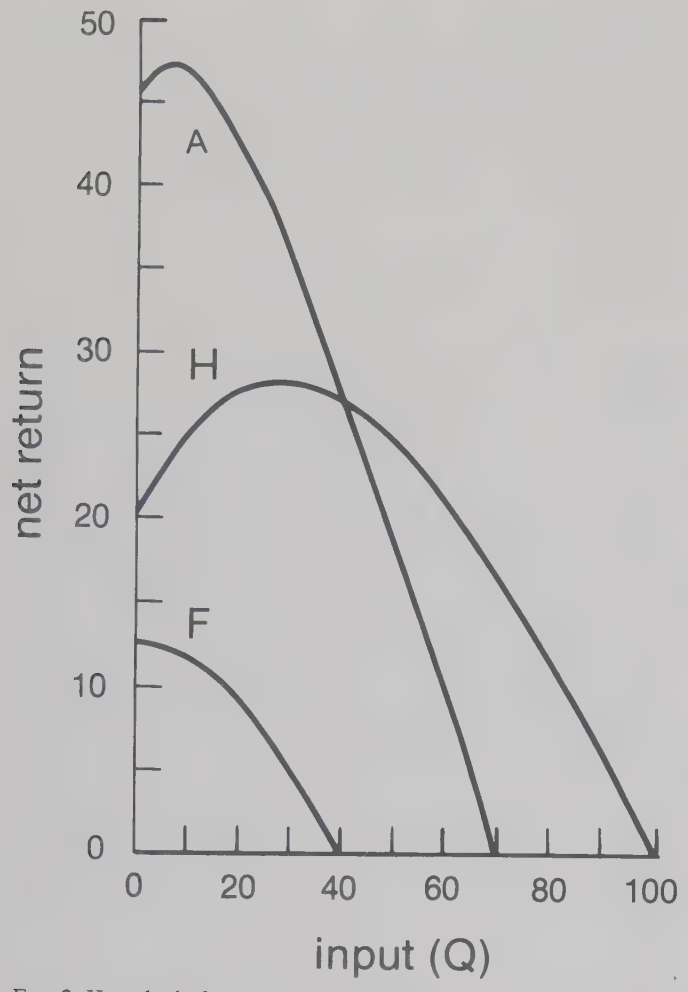

FIG. 2. Hypothetical net return ($Y_i - Q_i$) from the artisanal (A), high-input (H) and founder (F) breeds. The scaling of the axes is arbitrary (see text).

but the qualitative conclusion (breed A is more profitable than H over some range of Q) holds whenever strong GE interaction exists.

It appears that if specialized artisanal breeds can be developed, they can resist competitive displacement by high-input breeds under certain genetic and economic conditions. The most relevant external economic variable is probably the cost of input, m, expressed relative to the value of the yield. Substitution in Eqn. 1 followed by simplification yields

$$(2) \quad Y_i = \frac{C_i + gm}{a_i(C_i + gm) + b_i m}$$

which is solved for C_i, the cost of generating yield Y_i.

$$(3) \quad C_i = -\frac{m(Y_i(a_i g + b_i) - g)}{a_i Y_i - 1}.$$

Figure 3 shows the effect of variable input costs on the net return from whichever improved breed (A or H) generates the higher net return from a given input (Q). It is assumed that the farmer will choose the best available breed for each cost-input combination. The switch from the artisanal to high-input breed occurs at about 40 input units (visible as a bump in the isoclines in Fig. 3). Yield is calculated from Eqn. 1; variable cost from

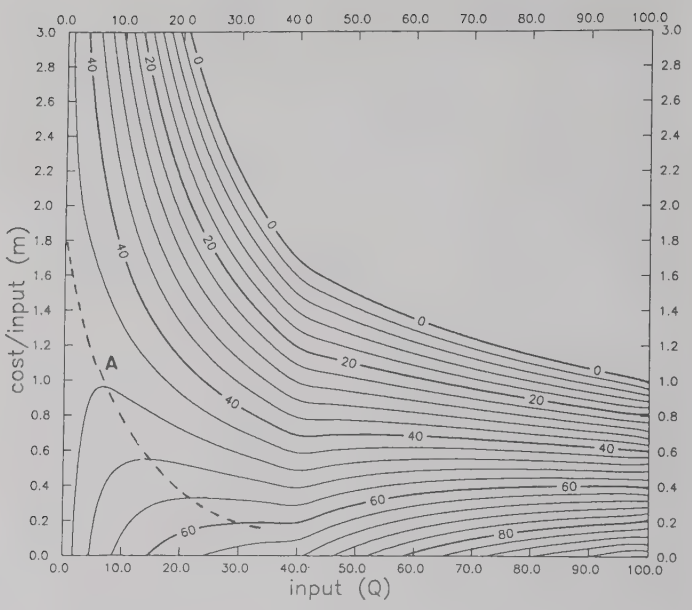

FIG. 3. Net return as a function of input and cost/input. Isoclines = net return calculated as in Fig. 2. Farmers switch to whichever breed maximizes net return as input rises or falls (breed A below and breed H above approximately 40 input units). Dashed line (labelled A) = approximate locus of point of maximum net return from the artisanal breed. Where the input cost is so low that the high-input breed is superior at all input levels, the locus of maximum net income is the right-hand margin of the diagram.

Eqn. 3. The input level (Q) and choice of breed (A or H) are the decision variables available to the farmer in Fig. 3. When the unit input cost, m, exceeds approximately 0.8, low input aquaculture with breed A generates the absolute maximum net return. In other words, when variable costs are high the artisanal breed may be absolutely resistant to competitive displacement. When costs are lower than about 0.5, breed H provides the higher absolute net return. However, use of the artisanal breed with low input remains more profitable for farmers unwilling or unable to grow H with at least 40 input units or so.

Under less severe economic conditions (lower m) the artisanal breed is still *relatively* stable, in that the farmer using breed H must add input above a threshold value to realize an increase in net returns. Note that the attractiveness of the artisanal breed increases rapidly as costs increase — *including the costs of externalities such as environmental pollution*. The conclusion is qualitatively robust for all parameter values that generate strong GE interaction.

It can be seen from Fig. 2 and 3 that strong GE interaction among breeds specialized for different input levels increases their resistance to economic exclusion. Low-input cultivation of the specialist breed is economically preferable over a broad range of input costs (Fig. 3). The overall objective of the selection programme, which is to increase aquaculture yield, is achieved, because both the artisanal and high-input breeds perform better than the founder strain in their respective aquaculture systems.

Our socioeconomic perspective evidently reverses the priorities of conventional genetic improvement programmes. In crop breeding, as already mentioned, elimination of GE interaction is the usual objective (Crossa et al. 1989; Rognli 1987; Baker 1988; Rosielle and Hamblin 1981). (The parallel objective in

aquaculture would be a variety of, say, tilapia, that shows improved performance in a range of Asian aquaculture systems.) We argue that if the usual animal breeding objectives are applied to aquaculture they are also likely to reduce both the genetic diversity of aquaculture stocks and the sociological diversity of aquaculture farming systems. A programme that deliberately selects for genetic diversity, on the other hand, could reduce the negative impact of modern aquaculture on both genetic and social diversity while maintaining a high rate of genetic gain. Indeed, selection that occurs at both the individual and population level can be significantly more efficient than selection at either level alone (Wade 1985). Selective diversification would also provide a short-term economic advantage to the individual farmer, which most genetic conservation proposals emphatically do not.

The economic simulation in Fig. 2 and 3 suggests that the economic advantage of this breeding policy accrues to the consumer of the new breeds (ie. to the farmer). The genetic diversification policy would appear to have little economic advantage to the breeder of specialized breeds, since the breeder sells to the farmer, and the market for any particular genotype would be comparatively small. The benefit to the breeder is negligible if the superiority of the breed is based on additive genetic variance and farmers multiply their own stock.

In this situation (where benefits accrue to the farmer or the ultimate consumer rather than the breeder) the organization of breeding programmes must come at the national or international level, rather than through the private investment of individual breeders (Smith 1978; Hill 1981). The specialized breeds must however be developed locally, perhaps through "farmer oriented" extension or research station activities utilizing reliable, small-scale genetic improvement procedures (e.g., Uraiwan and Doyle 1986). The high return from investment in genetic improvement that benefits farmers, when investment takes place at the national or supra-national level (Smith 1978), makes the "aquaculture gene centre" an attractive conservation strategy. Although it is admittedly a compromise from a purely genetic point of view, it does go some way towards reconciling the opposed objectives of increased aquaculture production and genetic conservation.

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Governmental Views and Regulations

Fish Introductions in Canada: Provincial Views and Regulations[1,2]

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The umbrella legislation governing introductions of fish and fish products to the provinces and territories of Canada is the Fisheries Act of Canada which provides for the making of regulations concerning coastal and inland fisheries. Specific jurisidiction over introductions for fish health reasons is included in the Fish Health Protection Regulations under the Fisheries Act. Most of the jurisdictions have enacted fishery regulations under the federal Fisheries Act which control movement of fish into their territories and between water bodies within their boundaries. Some jurisdictions have additional broad natural resources legislation which includes provision for regulating movement of introduced species. Specific policies concerning introduction issues have been developed in some jurisdictions and are being considered in others. Legislation and compliance efforts to prevent unwanted introductions have not been particularly effective. Recent attention, particularly in the Great Lakes basin, has focused on ballast water introductions with potential for considerable economic and ecologic damage (e.g. *Gymnocephalus cernuus*, *Dreissena polymorpha*). Neither federal nor provincial legislation appears to have sufficient scope to prevent or control this class of introductions.

La *Loi sur les pêches* est la loi générale qui régit l'introduction de poissons et de produits de la pêche dans les provinces et territoires du Canada et qui permet l'élaboration de règlements sur les pêches côtière et intérieure. Les *Règlements sur la protection de la santé des poissons* en vertu de *la Loi sur les pêches* prévoient d'autres instances pouvant réglementer l'introduction pour des raisons liées à la santé des poissons. La plupart des gouvernements provinciaux et territoriaux se sont dotés, dans le cadre de la loi fédérale sur les pêches, de règlements sur les pêches qui limitent l'introduction de poissons sur leur territoire et la transplantation d'un plan d'eau à un autre situés à l'intérieur de leurs frontières. Certains gouvernements possèdent d'autres lois plus générales sur les ressources naturelles qui comportent des dispositions sur la transplantation d'espèces introduites. Certains gouvernements ont défini une politique particulière concernant l'introduction de poissons et d'autres envisagent de le faire. Les lois, et les efforts déployés pour les faire respecter, n'ont pas été particulièrement efficaces pour prévenir l'introduction non voulue de poissons. L'attention s'est récemment portée, dans le cas du bassin des Grands Lacs en particulier, sur l'introduction, part les eaux de ballast des navires, d'espèces qui peuvent causer des dommages économiques et écologiques considérables (p. ex. : *Gymnocephalus cernuus, Dreissena polymorpha*). Il semble que ni la loi fédérale ni les lois provinciales n'aient la portée nécessaire pour empêcher que des poissons ne soient introduits de cette manière.

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Global concern about the introduction of exotic organisms into aquatic ecosystems has heightened in recent decades (Rosenfield and Mann 1991). Marine and freshwater ecosystems in North America have been particularly vulnerable to potential risks associated with introductions of fish and other aquatic organisms. Concern about ecological damage from "biological pollution" has been expressed in several recent symposia (Courtenay and Stauffer 1984; Kohler 1986; Sinderman et al. 1991). Warren (1971) defined water pollution as "any impairment of the suitability of water for any of its beneficial uses, actual or potential, by man-caused changes in the quality of the water." Although water pollution is generally considered in terms of chemical and physical additions or alterations, biological inputs are indeed capable of impairing beneficial uses.

Canada, with two sea coasts and an extensive inland waterway (the St. Lawrence Seaway) is especially vulnerable to unwanted introductions from global marine traffic. In addition, many species of fish have been moved (intentionally or unintentionally) within and between provinces and territories. Crossman (1991) has reviewed the history and pattern of fish introductions into Canadian waters. As of 1989, a total of 92 species and 13 subspecies or hybrids had invaded, been brought into or transferred within Canada. In the Laurentian Great Lakes alone about 41 species of fish have been introduced since the early 1800's either intentionally or unintentionally by man's activities (Emery 1985; Mills et al 1991). Some of the suc-

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cessful invaders (e.g. sea lamprey, *Petromyzon marinus*) have severely impacted native fish populations (Christie et al. 1972).

In this paper we briefly review legislation and policies of the provinces and territories of Canada with respect to introductions of fish species. We also attempt, in a general way, to consider the effectiveness of legislation in preventing unwanted introductions and transfers.

Fisheries Legislation and Policies

The Fisheries Act of Canada

The umbrella legislation governing introductions of fish and fish products to the provinces and territories of Canada is the Fisheries Act (R.S.C., 1985, c. F-14) which is administered by the Department of Fisheries and Oceans. The Fisheries Act provides for the making of regulations concerning coastal and inland fisheries including:

(a) the catching, loading, landing, handling, transporting, possession and disposal of fish;
(b) the taking or carrying of fish or any part thereof from one province to any other province;
(c) the conservation and protection of fish.

More specific jurisdiction over salmonid introductions is included in the Fish Health Protection Regulations under the Fisheries Act. The Regulations prohibit the importation of cultured fish, eggs of wild fish, or dead cultured salmonid fish species into Canada or between provinces without a permit. The import permit may only be issued where an applicant has obtained a fish health certificate from the facility from which the fish or eggs originated. This fish health certificate may only be issued to a facility which has been inspected for certain named fish disease agents, in accordance with the procedures outlined in *Fish Health Protection Regulations: Manual of Compliance*, Department of Fisheries and Oceans (1989).

Provincial Legislation and Policies

Canada consists of 10 provinces and two territories. The legislation and, in some cases, policies of these jurisdictions concerning the introduction of fish species are summarized in Table 1. As indicated above, the federal Fisheries Act is the principal piece of legislation governing provincial fisheries. Most of the jurisdictions have enacted fishery regulations under the Fisheries Act which are intended to control movement of fish into their territories and between water bodies within their boundaries (Table 1). In general, the regulations prohibit importation of live fish or eggs into, or transfer within, the jurisdiction except under the authority of a licence or permit issued by the Minister. Some jurisdictions (e.g. British Columbia; Manitoba) list the prohibited species in schedules.

In addition to legislation enacted under the federal Fisheries Act, some provinces (e.g. British Columbia, Ontario, Quebec, New Brunswick) have provincial legislation with specific sections pertaining to introductions (Table 1).

Use of live bait is recognized by most jurisdictions as a vector for unwanted introductions and, therefore, importation of fish species for this purpose is prohibited. In most areas of British Columbia, use of freshwater invertebrates or finfish and any product thereof (except roe) as bait is illegal. Alberta does not allow the use of live finfish for bait but leeches and worms are allowed. In Saskatchewan, use of live baitfish is prohibited but use of live leeches, worms, crayfish and preserved fish is allowed. Manitoba has prohibited the import of live bait and has banned its use in northern areas of the province. Use of live crayfish, leeches, earthworms or preserved bait is permitted. Ontario prohibits the imports of live bait but allows its use and transport within the province. Crossman (1991) listed six species of fish that are believed to have been introduced unintentionally into Ontario by release of live bait. The Ontario Ministry of Natural Resources is currently reviewing Ontario's live bait policy and regulations with a view to development of guidelines or revision of regulations to address this problem. There is concern that the existing ease with which live bait can be transported throughout the province could aid in the dispersion of the zebra mussel (*Dreissena polymorpha*), a recent invader of the Great Lakes, into inland waters. Quebec has established three bait zones in the province: use of live bait until 1993 when permission expires (St. Lawrence Valley), dead bait only, and no bait (dead or alive) permitted. Transportation of live bait outside of the St. Lawrence Valley is prohibited. New Brunswick prohibits the import of live bait but allows its use. An outright ban on live bait is being considered in recognition of potential ecological damage from release of bait in new waters. Newfoundland is also considering the prohibition of the use of live bait.

The strong influence of the Federal government in the formulation of regulations and policies pertaining to introductions is particularly obvious in jurisdictions adjacent to coastal waters. For example, the Department of Fisheries and Oceans' Rainbow Trout Policy establishes policy districts and outlines permitted uses in the Maritime Provinces. In Newfoundland, the Department of Fisheries and Oceans Policy for Introductions and Transfers of Salmonids permits only reproductively sterile rainbow trout in the province, except in one small defined area. In British Columbia, the Department of Fisheries and Oceans and the Provincial government have formed a Transplant Committee to consider all proposals for transplants and introductions.

Agreements with the Department of Fisheries and Oceans on aquaculture, fish stocking and fish health have been completed for seven provinces; they are under negotiation in three central provinces and the territories.

Efficacy of Regulations and Policies

This brief summary of jurisdictional legislation points to a maze of regulations and policies established across Canada with the intent to control intentional introductions and to prevent unwanted introductions of fish species. The need to regulate the flow of live fish and genetic material is based on economic and ecological considerations. Logically, regulation of the movement of live fish and genetic material should be based primarily on ecological considerations, i.e. economic benefits are dependent on healthy fish communities. Protection of fish health is a major criterion for the development of the regulatory apparatus; however, risks associated with the displacement of native stocks are also considered.

The aquaculture industry and programs to enhance sport fisheries have resulted in a number of introductions into or transfers within Canada that have been economically beneficial. Salmonids comprise the main target species but other types of finfish and invertebrates have been introduced.

How effective has existing legislation been in preventing the introduction of unwanted species? The record of invading species that have become established in Canada indicates how difficult it is to legislate against biological pollution. The federal

TABLE 1. Summary of fish introduction legislation and policies.

British Columbia

A. Legislation
   1. British Columbia Fishery Regulations
      — prohibits import of live fish in Schedule IV (52 taxa)
      — prohibits introduction, transfer or transport of live fish except under authority of a licence issued by the Minister.
   2. Wildlife Act
      — regulations under the Wildlife Act (B.C.) make it an offence to possess, transport or traffic in live freshwater finfish (goldfish and tropical ornamental fish are exempt) without a permit.

B. Policies
   1. To give first priority to protection, maintenance and enhancement of wild native fish stocks.
   2. To stock hatchery-reared or non-native species or races only according to approved fishery management plans.
   3. To obtain approval of the Federal/Provincial Transplant Committee before undertaking (a) any import of non-salmonids; or (b) any intraprovincial transplant or introduction of fish or aquatic invertebrates. (The Committee's main concern is disease transmission but genetic and ecological implications may be considered.)

Alberta

A. Legislation
   1. Alberta Fishery Regulations
      — a permit is required to import cultured fish or eggs into the province.

B. Policy
   — no official Provincial policy, but Fisheries Management Branch restricts stocking in certain areas and near hatcheries.

Saskatchewan

A. Legislation
   1. Saskatchewan Fishery Regulations
      — regulates introductions of live fish and live fish eggs through licence or written permission of the Minister. (applies to importation to the province and transfer within the province).
      — no import of fish for live bait (earthworms may be imported for live bait).

B. Policy
      — currently under development
      — in interim using a policy similar to the Environmental Policy Statement of the American Fisheries Society on Introduction of Aquatic Species.

Manitoba

A. Legislation
   1. Manitoba Fishery regulations
      — no import of live fish or eggs without permission
      — no import, possession or release of eggs or fish of species in Schedule IX:

bowfin	pallid sturgeon
gars	shortnose sturgeon
gizzard shad	shovelnose sturgeon
grass carp	smelts
herrings	Utah chub
paddlefish	walking catfish

      — no import of fish for live bait.

Ontario

A. Legislation
   1. Ontario Fishery Regulations
      — no transporting of live fish (other than bait fish) and no depositing of live fish from one body of water in the province to another without a licence
   2. Environmental Assessment Act
      — requires class environmental assessment for fish stocking in new waters
      — requires individual environmental assessment for stocking of exotic species

B. Policy
   1. Strategic Plan for Ontario Fisheries (SPOF)
      — focus is on native, naturally-reproducing species
   2. Policy on stocking of fish for artificial fishing opportunities (draft stage).

TABLE 1. (*Continued*)

Quebec

A. Legislation
   1. Loi Sur La Conservation De La Faune
      and
   2. Loi Sur La Conservation et La Mise en Valeur de la Faune
      — provides for conditions on the importation of fish (species and numbers transported)
      — conditions and regulations are under development; will include disease certification.

New Brunswick

A. Legislation
   1. New Brunswick Fishery Regulations
      — no introductions of non-indigenous species or cultured fish or eggs of wild fish, unless authorized
      — no importation of live bait.
   2. New Brunswick Fish and Wildlife Act
      — fish ponds regulation prohibits any species other than brook trout in commercial ponds
      — Federal importation permit and disease free certificate are required for importation of brook trout.

Nova Scotia

A. Legislation
   — Agreement with Department of Fisheries and Oceans is currently in negotiation.
   — Fish Health Protection Regulations apply.

B. Policy
   1. Region Fish Health Guidelines
      — prohibits movement of fish stocks from areas where there are known carriers of certain diseases to areas where the disease agent is not known to be present.
   2. Fisheries and Oceans Rainbow Trout Policy
      — describes policy districts in Nova Scotia, New Brunswick, and Prince Edward Island
      — outlines permitted uses by district.
   3. Guidelines for implementing the ICES Code of Practice Concerning Introductions
      — recommends steps for reviewing proposals for new introductions
      — includes a thorough evaluation of species life history, ecology, disease, etc.

Prince Edward Island

A. Legislation
   1. Fish and Game Protection Act
      — no imports of exotics without permission
      — no possession or release to wild of live non-native fish without permission.

B. Policy
   — to refuse all introduction requests.

Newfoundland

A. Legislation
   1. Newfoundland Fishery Regulations
      — prohibits importation of live fish into or transfer within the Province except with permission of the Minister.

B. Policy
   1. Introductions and Transfers Policy
      — transfers or introductions of fishes from outside North America or from west of the continental divide will not be approved
      — sets out conditions of licence for other transfers or introductions

Yukon

A. Legislation
   1. Yukon Fisheries Regulations
      — the introduction of live fish or fish egs into the Yukon Territory, the possession of live fish or fish eggs or the transfer of live fish or fish eggs from one body of water to another, within the Yukon territory, is prohibited, except by special permission of the Minister.
   2. A sub-agreement on aquaculture with the Department of Fisheries and Oceans is currently being negotiated.

B. Policy
   1. Anadromous Fish Stocking Policy

TABLE 1. (*Concluded*)

Northwest Territories

A. Legislation
   1. Northwest Territories Fisheries Regulations
      — no introduction of live fish or live fish eggs into any waters except under the authority of the Minister (by permit).

B. Agreements with Department of Fisheries and Oceans
   1. Agreement on Freshwater Aquaculture in the Northwest Territories
      — finfish must not be imported into the NWT without compliance with the federal Fish Health Protection Regulations
      — only those finfish designated in Schedule B (9 taxa — mainly Salmonidae) may be stocked for recreational purposes.
   2. Agreement on a Northwest Territories Recreational Fish Stocking Work Plan
      — to identify water bodies/systems with a potential for fish stocking
      — to supervise and monitor all fish stocking occurrences.
      — to determine growth, survival, and stocking rates.
      — to develop an Arctic char broodstock for recreational stocking.
      — to inform and educate the public on the program.

Fisheries Act, which is the principal legislation in Canada regulating introductions, has been in existence for about 130 years. Crossman (1991) recorded that by 1989 a total of 92 fish species had invaded, been introduced or transferred in Canada including 38 species from U.S. waters. Sixteen species of exotics had become established by 1989 (Crossman 1991). Emery (1985) listed 34 species which had been introduced into or had invaded the Great Lakes between 1819 and 1974, about one-half of which have become established. Mills et al (1991) added seven species which have entered the basin since 1974. Fish diseases, particularly furunculosis and whirling disease, have been introduced or transferred, probably in association with the movement of salmonids.

Crossman (1991) has warned that it is impossible to close the list of introduced fishes. Indeed, the rate of invasion of plants and animals has increased in recent decades. In a study of Great Lakes invasions, Mills et al. (1991) found that 46% of the approximately 127 species that have become established since 1810 have entered the system since 1960. The opening of the St. Lawrence Seaway in 1959 points to the importance of shipping as an entry vector. Approximately one-third of established invaders entered the Great Lakes in ballast water (Mills et al. 1991). This vector is considered to be responsible for the introduction in the 1980's of the ruffe (*Gymnocephalus cernuus*), the spiny water flea (*Bythotrephes cederstroemii*) and the zebra mussel. The ruffe could disrupt Great Lakes fisheries if it displaces yellow perch and feeds on whitefish eggs as it does in Europe (Pratt 1988). The spiny water flea has successfully invaded all of the Great Lakes and some inland waters. It has the potential to impact food web structure (Lehman 1988), but is also being consumed by some fish species and may not have a major impact on the Great Lakes ecosystem (Sprules et al 1990). The economic impacts of the zebra mussel are already substantial and will likely increase to hundreds of million dollars per year (IJC-GLFC 1990). Ecological impacts are as yet unknown but fish production could be affected through food-web alteration. All three organisms have the potential to spread over large areas of North America.

In 1990 small numbers of the tubenose goby (*Proterorhinus marmoratus*) and the round goby (*Neogobius melanostomus*) were found in the St. Clair River (David Jude, University of Michigan, Ann Arbor, MI, pers. comm.). Ballast water is the likely vector.

Existing legislative and regulatory efforts by the federal and provincial governments have been ineffective in preventing this class of introductions. However, recently the problem has attracted considerable attention which has resulted in new efforts to prevent ballast water introductions. In September 1990 the Great Lakes Fishery Commission and the International Joint Commission made a joint appeal to the governments of the United States and Canada to address the ballast water issue (IJC-GLFC 1990). The Commissions recommended that the governments of both countries require all ocean going ships to exchange ballast water in mid-ocean before entering the Great Lakes system or provide treatment to remove or destroy all organisms capable of surviving in the waters of the Great Lakes ecosystem. In November, 1990, legislation requiring mandatory compliance by the shipping industry with the ballast exchange was enacted by the United States (Public Law 101-646, Non-Indigenous Aquatic Nuisance Prevention and Control Act). Similar legislation is being considered in Canada. The Canadian Coast Guard currently coordinates a program of voluntary guidelines which encourages the shipping industry to exchange ballast waters. Compliance by the shipping industry with the voluntary guidelines is currently in excess of 90%. Ballast water may be the most manageable of all anthropogenic vectors for the introduction of new species. Ideally, a ballast water management plan would require incoming ships to provide full details of amount and location of ballast origin and exchange. Alternative methods of ballast water treatment would be required and provided (at the ship owners' expense) in cases of non-compliance with exchange regulations.

Carlton (1991) discussed the role of aquaculture and fisheries activities in the global homogenization of biota. He considered that the deliberate and accidental release of organisms by aquaculture and fishing industries is second only to shipping as an introduction vector. In their Great Lakes study, Mills et al. (1991) found that 32% of all successful plant and animal introductions were due to deliberate and accidental release, compared with 34% due to shipping. In the category of successful fish introductions, 35% were due to deliberate release, 27% were due to accidental release and 19% were due to shipping. Overall the impacts of some of the deliberate introductions (e.g. rainbow trout, *Oncorhynchus mykiss*) have been positive and others (e.g. common carp, *Cyprinus carpio*) have been negative. Carlton (1991) stated that global interest in aquaculture was increasing and would likely accelerate the rate of introduction of exotic species. Pressure in Canada for the introductions and transfer of new species for aquaculture and fishery

enhancement will likely continue to test the existing legislation. To date, this legislation has not been particularly successful in preventing and controlling the introduction of undesirable species. There appears to be a need for new and improved legislation, particularly to deal with unwanted species transported by the shipping industry. However, part of the failure of existing legislation to prevent and control introduction is due to insufficient commitment by jurisdictions to enforce regulations and to obtain compliance.

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U.S. Federal Policies, Legislation, and Responsibilities Related to Importation of Exotic Fishes and Other Aquatic Organisms[1,2]

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Within the Federal government, the U.S. Fish and Wildlife Service (Service) has primary responsibility for legal and policy responsibility for introduced exotic species. The Lacey Act of 1900 authorizes the Service to prohibit the importation of species that are potentially injurious to native fish and wildlife. However, regulations under authority of the Lacey Act cover only a few species. The Nonindigenous Aquatic Nuisance Prevention and Control Act of 1990 established a Task Force co-chaired by the Director of the Service and Under Secretary of Commerce for Oceans and Atmosphere. The Task Force consults with the Secretary of Transportation to develop regulations to prevent the importation and spread of aquatic nuisance species into the Great Lakes through exchange of ballast water. Federal agencies must comply with Presidential Executive Order 1198, Exotic Organisms, that prohibits Federal agencies or activities they fund or authorize from introducing exotic species. The Service conducts research and evaluation of exotic species to support Federal, State, and local efforts to prevent further importation of harmful species. Effective regulation will also depend on the full cooperation with Canada.

Au sein du gouvernement fédéral américain, la responsabilité première en matière de réglementation de l' introduction d'espèces exotiques incombe au FWS (Fish and Wildlife Service). La *Loi Lacey* de 1900 confère au FWS l'autorité nécessaire pour interdire l'importation d'espèces qui peuvent être nuisibles pour les poissons et la faune indigènes. Toutefois, les règlements découlant de la *Loi Lacey* ne s'appliquent qu'à quelques espèces. La *Nonindigenous Aquatic Nuisance Prevention and Control Act* de 1990 a prévu la création d'un groupe de travail présidé conjointement par un directeur du FWS et le Sous-secrétaire au Commerce (Oceans and Atmosphere). Le groupe de travail consulte le Secrétaire aux Transports sur l'élaboration de règlements visant à empêcher l'importation et la dissémination dans les Grands Lacs d'espèces aquatiques nuisibles par l'intermédiaire des eaux de ballast. Les organismes fédéraux doivent se conformer au décret présidential 1198 sur les organismes exotiques qui leur interdit d'introduire des espèces exotiques par leurs activités ou par les activités qu'ils parrainent ou autorisent. Le FWS procède à l'évaluation des espèces exotiques et exécute des travaux de recherche pour soutenir les efforts du gouvernement fédéral, des États et des autorités locales qui visent à prévenir d'autres cas d'importations d'espèces nuisibles. L'efficacité de la réglementation dépendra également de l'entière coopération du Canada.

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Introductions of non-native or exotic species and transfers of species between basins in North American waters generally are no longer activities of U.S. and Canadian Federal governments and State and Provincial agencies. Since the first importations three centuries ago (McCann 1984a), hundreds of aquatic species have been released into U.S. waters by the private sector and government agencies. Introduction of exotics peaked in the 1960's (Welcomme 1986). Recently, the private sector has been responsible for introductions of exotics, many of them unintentional. Now, introductions in ballast transport seem to be the most common mechanisms for transfers (Carlton 1985, 1989).

During the period in which deliberate importations took place, more than 126 exotic fishes were released in North America (Courtenay et al. 1984). Of these, at least 41 became established. More than 27 species have gained access to Canadian waters (Crossman 1991). Twenty species of fish have been transplanted into the Great lakes, mostly by deliberate stocking (Mills et al. 1991).

Disease organisms may accompany fish transfers, even those not destined for planting. Bacteria, viruses, and parasites were

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common in shipments of imported aquarium fishes (Shotts and Gratzek 1984). Many diseases were transferred with shipment of fishes (Hoffman and Schubert 1984).

Regulations of intentional and unintentional importations of aquatic organisms developed haphazardly. Prior to the 1960's, little concern was expressed regarding the possible detrimental effects of transfer of fishes. Agencies with the responsibility to protect biotic resources themselves were introducing exotic species. Only about 25 years ago, the potential for damage was generally recognized and U.S. Federal government and State agencies began developing policies and regulations for the control or prohibition of the importation of aquatic organisms (McCann 1984b). Such measures, however, were difficult to enforce because of wide open interstate commerce and a patchwork of State regulations in potential receiving States. In addition, user groups argued that tough preventive measure would stifle the pet trade and aquaculture. Furthermore, many professionals believed that exotic introductions were beneficial and ecological and genetic effects were vague and undocumented.

Only recently has the magnitude of introductions been systematically documented (Courtenay and Stauffer 1984). Although there were cases of clear detrimental effects, for most exotic introductions there was little data proving adverse consequences. Effects on the environment were no different for unintentional introductions than intentional ones (Carlton 1989). The Great Lakes have been invaded via ballast exchange by the zebra mussel (*Dreissena polymorpha*) (Hebert et al. 1989), the spiny water flea (*Bythotrephes cederstroemi*) (Bur et al. 1986), and the ruffe (*Gymnocephalus cernuus*) (Pratt 1988), all of which have potential for ecological disruption. Concern about plantings and unintentional release of exotic species is growing, even for fishes such as salmonids that in the past were widely planted (Porter and Goldthwaite 1987). The scientific and fishery management communities oppose unintentional introductions of non-native species and most now oppose intentional introductions. Introductions may even be considered pollutants (International Joint Commission 1987).

The purpose of this paper is to update the review by Clugston (1986), with new information about the statutory basis for U.S. Federal programs and policies about introduced exotic species. Stemming the tide of exotic introductions requires comprehensive enforceable regulations with deterrent penalties that include coordination of State, Provincial, and Canadian Federal agencies and the cooperation of the private sector. Education of the public to develop an ethic for environmental protection would enhance compliance.

U.S. Federal Statutes Related to Importation of Aquatic Organisms

Basic statutory authorities of the U.S. Fish and Wildlife Service have been interpreted as providing authority for the Federal government to engage in introductions. Based on several authorities such as the 1871 Act establishing the position of U.S. Fish Commissioner (16 Stat. 593, i.e., Volume 16, Statute 593 of Statutes of the United States of America) and the Fish and Wildlife Act of 1956 (16 U.S.C. 742a–742j, i.e., Volume 16 of the United States Code, Part 742a–742j), several exotic species of fishes and wildlife, such as common carp (*Cyprinus carpio*), brown trout (*Salmo trutta*), and grass carp (*Ctenopharyngodon idella*), have been introduced. Such legislation sanctions introductions of exotics by the Fish and Wildlife Service (Service), but hardly provides specific authority to prevent exotic introductions.

The most comprehensive Federal authority for controlling exotic introductions of fishes and other aquatic species is the injurious wildlife provision of the Lacey Act of 1900 with subsequent amendments (18 U.S.C. 42). In addition to prohibiting the intentional import of one genus and one species of mammal, the Lacey Act authorizes the Secretary of Interior to establish regulations controlling the import of other exotic species that have potential for harming humans, native fishes and wildlife, agriculture, horticulture, or forestry. Administratively established regulations are discussed in the next section.

The Fish and Wildlife Act of 1956 (16 U.S.C. 742a–742j) established a comprehensive national policy with guidance to the Fish and Wildlife Service. Among other things, the Secretary of the Interior is authorized to take steps "required for the . . . conservation, and protection of fisheries resources." These steps might include establishing policy to prevent introductions. To our knowledge this general provision has not been used.

The Endangered Species Act of 1973 (16 U.S.C. 1531–1543) has provisions for regulation of imports primarily to protect species from exploitation in their native range. Sections 7 and 10 prohibits an introduction if a case is made that U.S. endangered species would be further threatened. Fishes could not be stocked in the critical habitat of a listed species.

The Nonindigenous Aquatic Nuisance Prevention and Control Act of 1990 (104 Stat. 4761) authorizes the Secretary of Transportation to establish regulations in consultation with a Task Force co-chaired by the Director of the U.S. Fish and Wildlife Service and Under Secretary of Commerce for Oceans and Atmosphere (16 U.S.C. 4701–4741). Not later than 6 months after enactment, volunteer guidelines will be issued to prevent the introduction and spread of aquatic nuisance species into the Great Lakes through exchange of ballast water. Within 1 year, education and technical assistance are to be carried out to encourage compliance. Within two years, regulations for ballast exchange are to be issued. Anyone who violates the regulations is guilty of a class C felony and may be fined $25,000 U.S.

Administration of Statutes by the Fish and Wildlife Service

Regulations implementing the Lacey Act of 1900 are in 50 C.F.R. 16, i.e., Part 16 of Title 50 of the Code of Federal Regulations (1989). The present regulatory scheme allows the Service to directly control the importation of species that according to the regulations are potentially harmful. Harmful is defined in the Act as injurious to the health and welfare of humans, to the interests of forestry, agriculture, or horticulture, and to the welfare and survival of wildlife. The regulations contain a general prohibition of the importation of live wildlife, including fishes, mollusks, crustaceans, amphibians, and reptiles, and then exempts all but a few clearly undesirable taxa. This strategy for implementing the statute specifically lists a limited number of problem species and is often referred to as the dirty list approach. The list of injurious wildlife now includes 12 genera of mammals and 4 species of birds (50 C.F.R. 16.11). Among other taxa, injurious wildlife includes salmonid eggs or fish unless certified free of viral hemorrhagic septicemia and whirling disease (*Myxasoma cereloralis*) and any species of Clariidae. The mitten crab (*Eriocheir sinensis*)

is also on the list. Release into the wild is also prohibited except under State authority. Most species can be imported, transported, or possessed in captivity for scientific, educational, exhibition or propagation without a permit.

Several attempts in the 1970's to alter the strategy for implementing the injurious wildlife provisions of the Lacey Act ended in failure. These efforts were initiated under 50 C.F.R. 16 in which the Secretary of Interior may establish additional restrictions on imports. On December 20, 1973, the Service published a proposed rule (38 F.R. 34970, i.e., volume 38 of the Federal Register, page 34970) that concluded all exotics were potentially injurious and, except for several hundred taxa that were believed to pose little risk, should be prohibited. However, the more than 4 300 comments on this proposal, often referred to as the clean list approach, were mostly negative. A revised proposal, which greatly expanded the number of exceptions, was published on February 24, 1975 (40 F.R. 7935), and received 1 200 largely critical comments. Arguments against the two proposals cited insufficient evidence that importation of any particular species would be harmful. An economic argument was that the pet industry would have been particularly affected by excluding those rare or poorly studied species that command the highest prices. Consequently, the clean list strategy was not adopted.

In a further effort, a proposed rule (42 F.R. 12972) with a long list of potentially harmful taxa was published on March 7, 1977. Again, the hobby fish industry responded with many negative comments about this extensive dirty list. This effort at extending the dirty list was dropped as well, leaving only a few prohibited species under authority of the Lacey Act.

If the Lacey Act is to be effective in regulating exotic introductions, the dirty list of injurious species must be substantially increased or a clean list approach must be adopted. To be truly effective, Lacey Act provisions must be applied to all imports, including unintentional introductions, such as the discharge of untreated ballast water. Currently the Lacey Act addresses only intentional releases into U.S. waters and has no provisions for escaped exotics. The mitten crab, for example, is on the Lacey Act list, but incidents of invasions are likely to be by ballast transport (Bio-Environmental Services 1981).

The Nonindigenous Aquatic Nuisance Prevention and Control Act (16 U.S.C. 4727.1208) amends the Lacey Act (18 U.S.C.) 42(a)), by adding the zebra mussel as an injurious species. The Lacey Act did not anticipate a legislative mechanism for adding species to the dirty list.

The Nonindigenous Aquatic Nuisance Prevention and Control Act also has provisions for development of regulations other than for control of ballast. The Task Force established under the Act is authorized to develop and implement a program to prevent exotic introductions of aquatic nuisance species (16 U.S.C. 4722). If the Task Force determines that there is a substantial risk of an unintentional introduction by an identified pathway the appropriate Federal agency is authorized to act to minimize the risk of such an introduction. Within 1 year of enactment, the Task Force is to identify and evaluate approaches for reducing the risks of intentional exotic introductions.

Executive Order 11987 — Exotic Organisms

Although the U.S. government was unsuccessful in the 1970s at expanding control of exotic introductions, it, at least, ceased government sponsored exotic introductions. On May 24, 1977, President Carter signed Executive Order 11987 (42 U.S.C. 4321) to restrict introductions of organisms into or out of the United States by Federal agencies. For the first time the Federal government succeeded in establishing a policy that opposed all exotic introductions and not just a few. Federal agencies may not engage in transfers such as:

1. the introduction of exotic species into land and waters under their jurisdiction;
2. the importation of exotic organisms for introduction into any natural ecosystem of the United States; and
3. the export of native species for introduction into ecosystems outside the United States.

Exceptions to these restrictions can be made if the Secretary of Agriculture or Interior determines that the activity will not affect natural ecosystems. Although either agency head can approve exotic introductions, the Secretary of Interior was given the lead to develop regulations for implementing the Executive Order. The proposed regulations would have required that Federal and State agencies engaged in transplantation of exotic species must request a biological opinion from the Service. The requesting agency, of course, must provide adequate information to judge the effects of the proposed transfer. The Service would analyze the proposal and issue a biological opinion within 90 days. The Service implemented the proposed regulations by internal memorandum as guidelines for discharging its own responsibilities under the Executive Order. Other Federal agencies were not required to comply with the guidelines but must adhere to the requirements of the Executive Order itself. As a result of the guidelines, the intentional importation of exotic species by Federally sponsored programs has dropped to zero.

Federal agencies are supposed to encourage States, local governments, and private citizens to prevent exotic introductions, but an executive order, of course, cannot bind other organizations or individuals, unless they use Federal funds. The Service thus required that State agencies request opinions if they used Federal aid in a project involving exotic species. In several requests for biological opinions, the Service approved the research use of polyploid sterile grass carp. These sterile fish were being produced in this country and they posed minimal risk of becoming naturalized.

Exotic Species Research

Any agency with regulatory responsibility has an obligation to conduct research to appraise whether its regulations are effective and to identify new species or routes of entry that may need attention. The Service conducts such research on exotic species at several of its National Research Centers. The National Fisheries Research Center at Gainesville, Florida, has projects to identify and determine the distribution, status, and impacts of exotic species. This Center coordinates research on exotic species, serves as a clearing house for information exchange on exotic species, and welcomes information on the status of all exotic species in North America. One of its field stations, the Fish Farming Experimental Station in Stuttgart, Arkansas, conducts inspections of bioengineered exotic species, mostly grass carp, to certify whether they are triploid.

The National Fisheries Research Center—Great Lakes in Ann Arbor, Michigan, studies biology, distribution, and control of *Bythotrephes*, Asiatic clam (*Corbicula fluminea*), ruffe, and zebra mussels. The research conducted by the Great Lakes Center documented adverse ecological effects of invasions into the Great Lakes by the alewife (*Alosa pseudoharengus*), rainbow

smelt (*Osmerus mordax*), and sea lamprey (*Petromyzon marinus*).

The National Fisheries Research Center—LaCrosse, Wisconsin, and its Hammond Bay Biological Station, Michigan, have developed control techniques involving toxicants such as rotenone, antimycin, and lampricides. The current approach of both facilities is integrated management, in which sterile males, migration barriers, and trapping will be evaluated as a supplement to toxicants.

The Nonindigenous Aquatic Nuisance Prevention and Control Act authorizes funding of research on ballast transport, other pathways for introductions, assessment of risk, and evaluation of preventive measures. Early detection, monitoring, and dispersal after introduction are to be studied. Funding of control methods is authorized.

Future Federal Responsibility

The concern over introductions of exotic fishes and other aquatic organisms is acute. The recent invasions of European organisms (*Bythothrephes*, ruffe, and zebra mussels) into the Great Lakes has received considerable attention by Congress and the media. Current Federal regulatory frameworks are perceived as ineffective.

Transport of aquatic life in the ballast water of cargo vessels has a greater potential for introduction than any other process. In a study of 55 upbound transoceanic cargo ships sampled at Montreal, each ship with fresh or brackish ballast water had 5 to 48 species of algae and zooplankton and the number of individual live organisms of each species ranged from 10,000 to 8 billion per ship. Not only was the amount of ballast water massive, but these ships brought potential colonizers from throughout the world. Section 207 of Public Law 101-225, the Great Lakes Exotic Species Prevention Act of 1989, directed the U.S. Coast Guard to report to the Congress on means for preventing the introduction of exotic species into U.S. waters via ballast water discharges. That report recommended ballast water exchange at sea as the most attractive means to reduce the likelihood for introductions (U.S. Coast Guard 1990). The Nonindigenous Aquatic Nuisance Prevention and Control Act of 1990 authorizes the Secretary of Transportation to develop regulations to prevent the introduction and spread of aquatic nuisance species into the Great Lakes through ballast water (16 U.S.C. 4711). Regulations are to be issued by November 29, 1992. While an important step, such a procedure can only be part of a coordinated program to eliminate unplanned introductions. If we are to manage introductions of exotics, regulation of ballast must be a high priority.

Professional Responsibilities

In this paper, we summarized the role of the Fedral government in importation of exotic species. A broader issue is the role of exotic species in aquaculture, fisheries management, and the pet trade. How do we treat exotics that have already become established or that are widely used? Transplantation of fish and stocking of hatchery fish into ecosystems where they do not occur is widely practiced, including by the Federal government. Aquatic scientists have not been in agreement about the effects of these kinds of uses. Many believed that the benefits to aquaculture, fisheries management, and the pet trade far exceeded the possible harmful effects to natural ecosystems. Professional opinion has yet to reach consensus about the nature of the problem of transplants. Aquaculture will continue to use species that command high market prices and the pet trade will continue to deal in species that appeal to the consumer.

Policy makers and scientists should be aware that support for preventive measures is rarely available before the fact. Unplanned or ill conceived planting decided by local officials or private citizens, may become naturalized and become pests. Ideally, an enterprise that brings exotic species into an area should be required to minimize risks for escape.

Although progress has been achieved in defining the issue of exotic introductions, much needs to be accomplished. In developing policy recommendations for then President-elect Bush, the conservation community produced a *Blueprint for the Environment* (Anonymous 1989) that proposed a national meeting to reach a consensus on the problem of introductions. The American Fisheries Society through its Introduced Fish Section has promoted understanding of introduced species. The proceedings of a symposium on the distribution, biology, and management of exotic species was published (Courtenay and Stauffer 1984). The American Fisheries Society defined the terminology so communication was improved (Shafland and Lewis 1984). The American Fisheries Society established a policy on introductions of aquatic species (Kohler and Courtenay 1986). The Society held special sessions to consider *Strategies for Reducing Risks from the Introduction of Aquatic Organisms* (at the 1984 Annual Meeting), *Quantitative Effects of Introduced Organisms* (at the 1988 Annual Meeting), and *Zebra Mussel Ecology and Impacts* (at the 1990 Annual Meeting). Other groups sponsored four workshops on zebra mussels and one on ballast water monitoring. A working group of the Marine Environmental Protection Committee of the United Nation's International Maritime Organization is addressing the problem of international transfers.

Rigorous review of all exotic introductions and consultations of all concerned jurisdictions and user groups should precede any planned introduction. Finally, it is clear that success in such an endeavor depends on full cooperation among State, Provincial, Canadian, and international commissions — including various agencies within each governmental unit.

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U.S. State's View and Regulations on Fish Introductions[1]

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A survey of the policy of 50 U.S. states on transplanted fish introductions and stocking fish of different genetic strains indicates that all 39 responding states control exotic introductions. While 67% of the responding states restrict in-state movement of fish species, more attention is being given to restricting in-state strain movement. More needs to be done. Native species are stocked on top of reproducing populations and moved among watersheds; exotic species are introduced. In some cases, these stockings have appeared to benefit all interested parties, while in other circumstances exotics have totally disrupted ecosystems and become pests. These introductions and stockings are a combination of the fish being available, misunderstanding by managers of possible effects, and strong political pressure to satisfy anglers in more and more waters. Many times, little attention is given to the effect of these introductions on the native biota and fauna as it is perceived that stocking fish is a good thing. It is not until problems develop or anglers want another species added that the wisdom or success of these stockings is questioned. Minnesota's policy is that fish are not moved between watersheds until genetic similarities of the various species in the different watersheds are demonstrated.

Une enquête auprès de 50 États américains sur leur politique en matière de transplantation de poissons et d'empoissonnement avec des lignées génétiques indique que les 39 États ayant collaboré à l'étude limitent l'introduction des espèces exotiques. Même si 67 % de ces États limitent déjà la transplantation des espèces de poissons à l'intérieur de leurs frontières, on songe maintenant à étendre cette mesure à la lignées. On doit cependant faire plus. Des espèces indigènes sont ajoutées à des populations qui se reproduisent ou sont transplantées d'un bassin hydrographique à un autre; des espèces exotiques sont introduites. Dans certains cas, ces empoissonnements semblent avoir été profitables à toutes les parties en cause, alors qu'en d'autres occasions, les espèces exotiques ont perturbé l'équilibre des écosystèmes et sont devenues nuisibles. Introduction et empoissonnement résultent de la combinaison de divers facteurs : accessibilité des poissons, gestionnaires qui comprennent mal les effets possibles; fortes pressions politiques exercées par les pêcheurs. Dans bon nombre de cas, on porte peu d'intérêt aux effets de l'introduction de poissons sur la biocénose indigène, car l'empoissonnement est perçu comme une bonne chose. C'est uniquement lorsque des problèmes surgissent ou que des pêcheurs souhaitent l'introduction d'une autre espèce que l'on remet en question la sagesse ou la valeur de cette activité. Au Minnesota, la politique consiste à ne pas transplanter de poissons d'un bassin hydrographique à un autre avant qu'il ait été démontré que les diverses espèces des différents bassins sont génétiquement semblables.

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Fishery managers, in their quest to satisfy anglers, are often guilty of oversimplifying their view of an ecosystem in an attempt to rationalize the negative effect stocking may have on the long-term stability of the ecosystem. If fish managers cannot find a major negative to the stocking, they rationalize that it will not harm the ecosystem. Many times these stockings in "unoccupied" niches cause declines in populations of native species. A case in point would be the decline of a trophy lake trout, *Salvelinus namaycush*, fishery in Saganaga Lake after stocking walleye, *Stizostedion vitreum vitreum*, in the late 1930's and early 1940's (MN DNR Lake Files, St. Paul, MN, unpubl. data). Only today is the lake trout population recovering and then only after a decline in the walleye population.

Introductions have been made by state management agencies, through accidental aquaculture escapees, aquarium releases, and by "bait bucket" releases. In some cases, the stocking has been carefully reviewed beforehand while in others releases have been made by well intentioned anglers with no thought of the consequences. It has been hypothesized by Minnesota fish managers that rainbow smelt, *Osmerus mordax*, were introduced into inland waters in Minnesota by an angler who caught fish in Lake Superior and cleaned them on his dock (MN DNR Files, St. Paul, MN, unpubl. data). The advent of live wells in fishing boats has improved the success of "bait bucket" introductions by providing a more hospitable transfer environment for the target species.

From some view points there are success stories with introducing exotics. These include the brown trout, *Salmo trutta*, striped bass, *Morone saxatilis*, Pacific salmon, *Oncorhynchus* spp., and steelhead rainbow trout, *O. mykiss*. While these have been considered successes, they have not been without adverse effects on native species. An example would be of brown trout out competing brook trout (Waters 1983). The most notable pest that has been introduced has been the common carp, *Cyprinus carpio*. Some introductions such as the opossum shrimp, *Mysis relicta*, and rainbow smelt have received mixed reactions from people evaluating them (Evans and Loftus 1987; Richards

[1]This paper forms part of the Proceedings of the Ecological and Genetic Implications of Fish Introductions Symposium (FIN) convened at the Great Lakes Institute, University of Windsor, Ontario, Canada, May 17–19, 1990.

et al. 1975). Time will resolve whether these introductions can be termed beneficial.

Of more concern today are the perils associated with the commercial aquaculture industry. The pressure exerted by this industry to have the right to farm any species regardless of possible negative outcomes is awesome. This pressure is fueled by the potential monetary rewards available in this industry. Additionally, the industry is giving little attention to the possibility of disease organisms being relocated without anyone's knowledge or to the ability to treat these diseases. Minnesota currently has no pathogens present for viral hemorrhagic septicemia (VHS), infections pancreatic necrosis (IPN), or infectious hematopoietic necrosis (IHN), but with unlimited movement of fish into the state for food production this could change to the detriment of the sport fishing and commercial industries. Effects of disease or a new exotic species escaping from a commercial facility could be catastrophic to wild resources and the commercial industry.

Fish Policy

All states are concerned with introductions of new fish species by anyone outside their agency. A letter was sent to all 50 U.S. states querying them about their policy toward exotic introductions and their position, if any, on fish stocking based on genetics and strains (Table 1). Introductions of exotics into the waters of all 39 responding states are controlled by statute or internal policy. Iowa is an example of a state that has no statutory authority, but they are able to prohibit the importation of various species deemed harmful to the environment by administrative policy. Alternatively, other states can require further research or an environmental impact statement. Many times these regulations are circumvented by political pressure groups who think that the agency is being unduly restrictive. In the early 1980's, Minnesota DNR was pressured to unsuccessfully introduce striped bass into the Mississippi River. Walleye have been stocked into many bass–panfish lakes in Minnesota because of political pressure. The most commonly banned species, among the replying states, were grass carp, *Ctenopharyngodon idella*, and walking catfish, *Clarias batrachus*.

The farming of trout, salmon and various warm water species, while accepted by most states, is a source of major concern to state management agencies because of the possible introduction of disease organisms. In many states, these diseases could severely curtail ongoing fish management programs by both state and private facilities. Because of this many states restrict the importation of fish and eggs. In Minnesota, the DNR is selling eggs and fry to the private sector to minimize the possibility of disease introduction. This improves relationships with the private sector and allows some monitoring of which strains, species and diseases are present in the private sector.

In the past, agency introductions have been among the most harmful. Agencies are often guilty of supporting the introduction of an exotic in response to habitat degradation which has limited native species and/or as an alternative species to those already present. An example of this would be the zander, *Stizostedion lucioperca*, recently introduced by North Dakota. This species was to be a substitute for walleye.

The newer issue brought about by geneticists is whether it is important to preserve genetic integrity of strains as well as species. Genetic techniques have been used to catalogue native stocks, to evaluate their cladistic relationships, to estimate time of divergence into various taxonomic branches and to determine the genetic diversity of species (Wattendorf and Holcomb 1986). Some genetic techniques now used in fisheries include stock characterization, selective breeding, and hybridization (Wattendorf and Holcomb 1986). The rapidity of these developments and the lack of understanding of the techniques by management agencies has left them in a quandary as to how to respond to this information. Some are embracing it and moving ahead while others are waiting to see what will happen in the future.

Florida and Alaska have very specific policies governing genetic integrity and strains of fish (Table 2). Twenty other states have a written or internal policy on in-state fish stocking. Florida has particular reason for being a leader in this area because of concerns for their varied resource, the potential for many negative changes in their native fauna, previous and ongoing problems with exotics, and because of personnel having a particular interest. Other states should follow their lead for similar reasons. Alaska has also promulgated an extensive policy on fish stocking to protect their native resource from the genetic contamination that has been seen in the lower 48 states. Several eastern states have no concerns about genetic integrity as they have stocked all species of fish for years and see no reason to change now. They feel the damage has already been done. In some senses they are probably correct in that stocking could have irreversibly altered native fish gene pools, but they cannot be certain until definitive studies have been completed.

More than 50% of the replying states have a policy on movement of fish with regard to genetic strain (Table 3). Most of these policies are for endemic populations that are in danger of being lost or that are being rehabilitated. Examples of these species include striped bass, Yellowstone cutthroat trout, *Oncorhynchus c. bouvirri*, Westslope cutthroat trout, *O. c. lewsi*, Colorado river cutthroat trout, *O. c. pleuriticies*, native cutthroat trout, *O. clarki*, muskellunge, *Esox masquinongy* and Florida largemouth bass. Most other states expressed concern about genetic integrity but have not progressed to the stage of implementing any policy or regulations. Genetic policies in some states will soon be forthcoming when current genetic research is completed while in others it will take longer. In many cases, change to more stringent stocking policies is viewed with concern by anglers as they perceive the loss of

TABLE 1. Questionnaire sent to 50 State Fisheries Chiefs querying them on fish stocking and fish genetics.

1.	Do you have concerns with fish stocking impacting the genetics of native fish stocks as we transplant fish from different watersheds, expand the range of native stocks, or stock the same species from a more northern or southern latitude?
2.	How are you handling fish transplants in regard to genetic integrity?
3.	What rules or regulations do you currently have and/or proposed to deal with these concerns?

TABLE 2. Status of laws and policies in responding states affecting in-state fish movement based on genetics.

STATE	States with laws	States with policy	Restrict in-state fish movement
Alaska	N	Y	Y[m]
Arizona	N	Y	Y
Arkansas	N	Y	Y[m]
Connecticut	N	—[q]	—[q]
Delaware	N	Y	N
Florida	N	Y	Y
Hawaii	N	N	N
Illinois	N	Y	Y[a]
Indiana	N	Y	Y[a]
Iowa	N	Y	Y[o]
Kansas	N	N	N
Kentucky	N	N	Y[b]
Louisiana	N	N	N
Maryland	Y	N	Y[d, f, h, n]
Massachusetts	N	N	N
Michigan	N	Y	Y[i, o]
Minnesota	N	Y	Y[a, b, c, o]
Missouri	N	Y	Y[l]
Montana	N	Y	Y[j]
Nebraska	N	N	N
Nevada	N	Y	Y[e]
New Hampshire	N	N	N
New Jersey	N	N	N
New Mexico	N	N	Y[k]
New York	N	Y	Y[d, o]
North Carolina	N	Y	Y[d, g]
Ohio	N	N	N
Oklahoma	N	Y	Y[l]
Oregon	N	Y	Y
Pennsylvania	N	Y	Y[d, p]
South Carolina	N	Y	Y[d]
South Dakota	N	N	N
Texas	N	N	N
Utah	N	N	Y[c, j]
Vermont	N	N	N
Washington	N	Y	Y
West Virginia	N	N	Y[b, g]
Wisconsin	N	Y	Y[b, o]
Wyoming	N	Y	Y[j]

[a]Largemouth bass, [b]Muskellunge, [c]Smallmouth bass, [d]Striped bass, [e]Native trout, [f]Brown trout, [g]Brook trout, [h]White perch, [i]Steelhead rainbow trout, [j]Cutthroat trout, [k]Indigenous species, [l]Broodstock, [m]Interregional, [n]Rainbow trout, [o]Walleye, [p]Lake trout,[q] Unable to determine.

angling opportunities through less stocking. Better education of anglers is needed so that they will work in partnership with state resource agencies.

Many states restrict in-state movement of species such as walleye, muskellunge, largemouth and smallmouth bass, *Micropterus dolomieui*, rainbow trout and brook trout, by watershed to reduce the possibility of contamination of the gene pool. Iowa policy specifically prohibits the stocking of lake spawning walleye into streams and stream spawning walleye into lakes because they have found that these stockings contribute little to the fish population, to the angler, and to the gene pool (Paragamian 1988). As more becomes known about the desirability of maintaining the genetic integrity of fish stocks, state agencies will likely become more sensitive to the issue. In some cases it may be too little, too late, because the state management agency has already moved native fish species among the various watersheds. In a few cases, politics may preclude the desirable biological decisions.

TABLE 3. Summary of status of laws and policy in responding states affecting in-state fish movement based on genetics.

Response	Number of states with law (%)	Number of states with policy (%)	Number of states that restrict in-state movement of species (%)
Yes	1 (2)	22 (44)	26 (52)
No	38 (76)	16 (32)	12 (24)
No response	11 (22)	12[a] (24)	12[a] (24)

[a]Unable to determine Connecticut's response so counted as no response.

Minnesota Examples

Minnesota has a checkered past in dealing with exotic introductions. The state management agency introduced brown trout, rainbow trout, steelhead rainbow trout, chinook salmon, *Oncorhynchus tshawytscha*, pink salmon, *O. korbuscha*, coho salmon, *O. kisutch*, striped bass, Atlantic salmon, *Salmo salar*, smelt, opossum shrimp and carp. Some such as the striped bass and inland stockings of Pacific salmon have not succeeded. Others, such as the brown trout, have succeeded quite well but at the expense of the native brook trout, *Salvelinus fontinalis* (Waters 1983). In spite of this successful competition with a native charr, brown trout are considered a successful introduction. Future exotic introductions in Minnesota waters will be subjected to greater scrutiny and control by the DNR than in the past.

Salmon introductions into Lake Superior have brought tremendous economic gain to communities near the lake. In Duluth, economic value of the sport fishery increased from near zero in 1976 to $3.5 million today in direct expenditures and over $9.0 million in related expenditures (U.S. Fish and Wildlife Service 1988). There are concerns, however, that these introductions may adversely effect the forge base and/or the rehabilitation of lake trout populations (Hanson 1990). It is too early to know if these introductions will be considered a success or another example of good intentions gone awry.

Current laws in Minnesota regarding fish introductions are only as good as the public will allow. For example, by policy, *Tilapia* spp. were not allowed in the state for commercial production without a permit. When politicians became involved with an entrepreneur who wanted to raise *Tilapia* spp., the state was forced to grant a permit. To date, there have been no problems with escapes. The present political climate in Minnesota and most other states often precludes good biology when evaluating species allowed for culture. Unfortunately, the power of the dollar often overwhelms good resource decisions. A more enlightened climate is necessary if we are to have sound resource management into the 21st century.

Minnesota has been like most states in that until recently stocking was done without regard for genetics. Walleye have been moved extensively around the state since the beginning of the hatchery system in the early 1900's. Additionally, walleye from all sources have been shipped to any requesting state. Walleye fry and fingerlings have been stocked on an as available basis so that all possibilities of fish source and receiving waters have probably been used. In site of this unhindered

stocking policy, some populations do appear to be slightly different genetically from others even though they have been stocked from the same sources (Murphy and Lee 1986; Fulton et al. 1991). Until more is learned about these walleye stocks, these systems will be stocked only with progeny from their respective systems. Muskellunge stocked in Minnesota have historically been derived from progeny from Shoepack Lake in the Kabetogama Peninsula near the Ontario–Minnesota border. Work by Post and LeGrande (1982) showed genetic differences between muskellunge from Shoepack Lake and Leech Lake. Additionally, these fish exhibit different color patterns, habitat requirements, and spawning requirements. Preliminary information from further studies has shown that Leech Lake fish grow faster and possibly achieve larger sizes (J. Younk, MN DNR, Bemidji, MN, pers. comm.). With this preliminary information, Minnesota has terminated use of all Shoepack Lake muskellunge and is using exclusively the progeny of Leech Lake or F1 Leech Lake broodstock for all muskellunge stockings. The genetic work on this species has enabled Minnesota to use a strain that grows faster and appears to achieve a larger size.

Additionally, Minnesota is not allowing any non-Hudson Bay drainage walleye to be stocked into the Hudson Bay drainage. Similarly, walleye stocking in the northern third of Minnesota requires a special permit if the walleye are from outside this area. In most cases, this permit will not be issued. Florida largemouth bass are not currently permitted in the waters of the state in spite of the desire of anglers. Smallmouth bass from lakes are not stocked into streams and those from streams are not stocked into lakes. Non-native channel catfish, *Italurus punctatus*, strains are not stocked into the St. Louis and Red River drainages. Work is ongoing to investigate these species for strain differentiation so that a more informed management program can be implemented. The paper by Philipp et al. (1983) has been instrumental in creating an awareness of the hazards of species and strain movement. The largest problem in strain differentiation work is funding the needed quality and quantity of work. Oftentimes programs of this type have a low priority for funding, precluding their implementation in a timely manner.

Discussion

If fish introductions and in-state fish transfers are not controlled by the states, we can expect to see a greater transmission of disease organisms, native species being displaced by exotics, and gene pools of native species being altered to the extent that they may not be as successful in their environment as the original strain. State biologists must be more attuned to the effects of fish transfers on forage and on non-fish organisms. In many cases, a common food source is utilized by other organisms as well as by the introduced fish. In other cases, fish such as grass carp consume the same aquatic vegetation as needed by waterfowl.

Perhaps the biggest danger management agencies face in introducing fish is the possible impact on forage and nongame species. Oftentimes introductions are made that ignore these organisms. Fish managers must consider the whole ecosystem instead of just sport fish, the monetary impact (benefit: cost analysis or effect on the economy), or pressures from constituent groups.

In many cases, stocking is done because it sounds good or there are fish available for this purpose. Good community ecology is forgotten! Socioeconomic reasons often hinder good biology. Much walleye stocking in Minnesota is not needed but is done because of social, political and economic pressures. Many lakes are stocked with walleye to the detriment of other game species. River run walleye stocks are used in lakes without large rivers. To date, it is not definitively known if river run walleye progeny will successfully spawn in a lake or if they contribute to the angler's bag. The salmon stockings in Lake Superior may be a mixed blessing as they may compete for forage with the lake trout which is being successfully rehabilitated. The biologist's job in the 1990's may be to educate anglers and politicians on good fish management philosophy; to educate them on the value and detriment of fish stocking in general and on introduced species and genetic strains in particular; to educate them on ecosystem management for all species instead of a favored one or two; and to educate them on the value of habitat preservation and enhancement. Careful community evaluation is a must if we are to have successful natural resource management. The condition of tomorrow's aquatic resources depend on today's actions. Now is the time to move into the 21st century.

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Meeting the Challenge of Exotics in the Great Lakes: the Role of an International Commission[1]

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The Great Lakes Fishery Commission has traditionally supported the conservation of genetic diversity native to the Great Lakes, and counseled caution in adding new species to the Great Lakes aquatic community. Since extinction of sub-specific taxa and establishment of new species in the Great Lakes have proven irreversible, caution and conservatism are warranted. The Commission's mandate has served the Great Lakes well in preventing, controlling, and managing exotics. For example, the Commission (1) provides a forum for interjurisdictional consultation prior to planned introduction of new fish species; (2) represents fishery agency concerns for inadvertent introductions to outside interests, as in the case of ship ballast introductions; (3) champions the conservation of genetic diversity native to the Lakes; and (4) controls the exotic sea lamprey at levels which permit fishery agencies to attain their fish community objectives.

Depuis toujours, la Commission des pêcheries des Grands Lacs a apporté son appui aux efforts visant à maintenir la diversité génétique naturelle dans les Grands Lacs et a prêché la prudence dans l'introduction de nouvelles espèces dans la communauté aquatique des Grands Lacs. Depuis qu'on a démontré que l'extinction de certaines sous-espèces et l'établissement de nouvelles espèces dans les Grands Lacs sont irréversibles, la prudence est de mise. Le mandat de la Commission lui a permis de prévenir l'introduction d'espèces exotiques ainsi que de surveiller et de gérer les espèces introduites, pour le plus grand bien des Grands Lacs. Ainsi, la Commission intervient de diverses façons : (1) elle offre aux différentes autorités un forum pour se consulter avant l'introduction planifiée de nouvelles espèces de poissons; (2) elle fait valoir auprès des intérêts étrangers les préoccupations des organismes de gestion des pêches face à l'introduction accidentelle d'espèces nuisibles, par exemple, l'introduction par l'intermédiaire des eaux de ballast; (3) elle se porte à la défense de la diversité génétique naturelle des Grands Lacs; et (4) elle limite la quantité des lamproies de mer exotiques à des niveaux qui permettent aux organismes de gestion des pêches de restaurer la communauté de poissons originale.

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Mandate

The Governments of Canada and the United States periodically considered the need for an entity such as the Great Lakes Fishery Commission (GLFC) throughout the first half of the century. However, it was the devastation wreaked on Great Lakes commercial fisheries by the invading sea lamprey in the 1940's and 1950's (Smith and Tibbles 1980) which provided a final compelling reason to proceed. The Governments of Canada and the United States of America signed the Convention on Great Lakes Fisheries establishing the new Commission in 1955 (Great Lakes Fishery Commission 1956).

To the credit of Convention negotiators, they avoided the temptation to limit the new Commission to minimizing or eradicating sea lamprey, currently its only management responsibility. Instead the first duty of the Commission is to investigate and advise Governments on measures to address issues affecting fish stocks of common concern to Great Lakes fisheries. However, concerned as they were for the troubled commercial fishery, U.S. and Canadian negotiators did not anticipate needs of raw water users and other emerging users of the resource (such as sport fishing, shipping, and recreational boating), which could be adversely impacted by changes in the aquatic community including fish.

In the 35 years since the Convention was signed, Commissioners and program auditors have concluded that the Commission's mandate is adequate for the needs of the Basin. However, casting about in 1990 for a suitable vehicle to coordinate management of the newly arrived zebra mussel (*Dreissena polymorpha*) (Hebert et al 1989), the U.S. Government found that the Convention as written did not permit a Commission role except where the zebra mussel threatened fisheries.

Because aquatic organisms introduced into the Great Lakes with ballast water discharged by oceangoing vessels were perceived as a threat to fish stocks of common concern (Dochoda 1989), the Great Lakes Fishery Commission was within its mandate advising Governments in 1988 and 1990 (IJC and GLFC 1990) on the risks to the fishery posed by exotic organisms, and recommending mid-ocean exchange as a preventive measure. Although not required by its mandate, the Commission also advised Governments of the risk posed by the ballast-introduced zebra mussel for other uses of the Great Lakes including navigation and drinking water. However, the Commission's experience in controlling exotics such as the sea lam-

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prey (*Petromyzon marinus*) was not tapped by Governments needing to coordinate research and control efforts on the zebra mussel. Concerned with the zebra mussel's potential to impede raw water use through colonization of intake pipes and to spread beyond the Great Lakes, Governments chose not to utilize the GLFC except for a minor consultation role in the U.S. on effects of filter-feeding, encrusting zebra mussels on food webs and fish spawning substrates.

Working Components of an International Commission

There are currently six groups or categories of membership (Fig. 1) operating under the umbrella of the Great Lakes Fishery Commission. First are Commissioners, four from each country (plus a U.S. alternate), appointed by the American President and Canadian Privy Council. Commissioners determine policy and provide long term direction, as well as participating individually in numerous activities conducted under Commission auspices.

The staff (or Secretariat) administers the Commission's program, providing liaison, support, and institutional memory throughout the committee system. As in most organizations, the Commission has most direct control over activities of its staff.

The Commission fulfills its management responsibilities, that is, control of the exotic sea lamprey, through contract with the U.S. Fish and Wildlife Service and Fisheries and Oceans Canada (referred to as the Commission's "Agents"). The Commission provides authority, program goals, funds, and accountability (but not day to day input) in the conduct of the sea lamprey control program.

Next are advisory boards such as the Habitat Advisory Board, Sea Lamprey Integration Committee, and Board of Technical

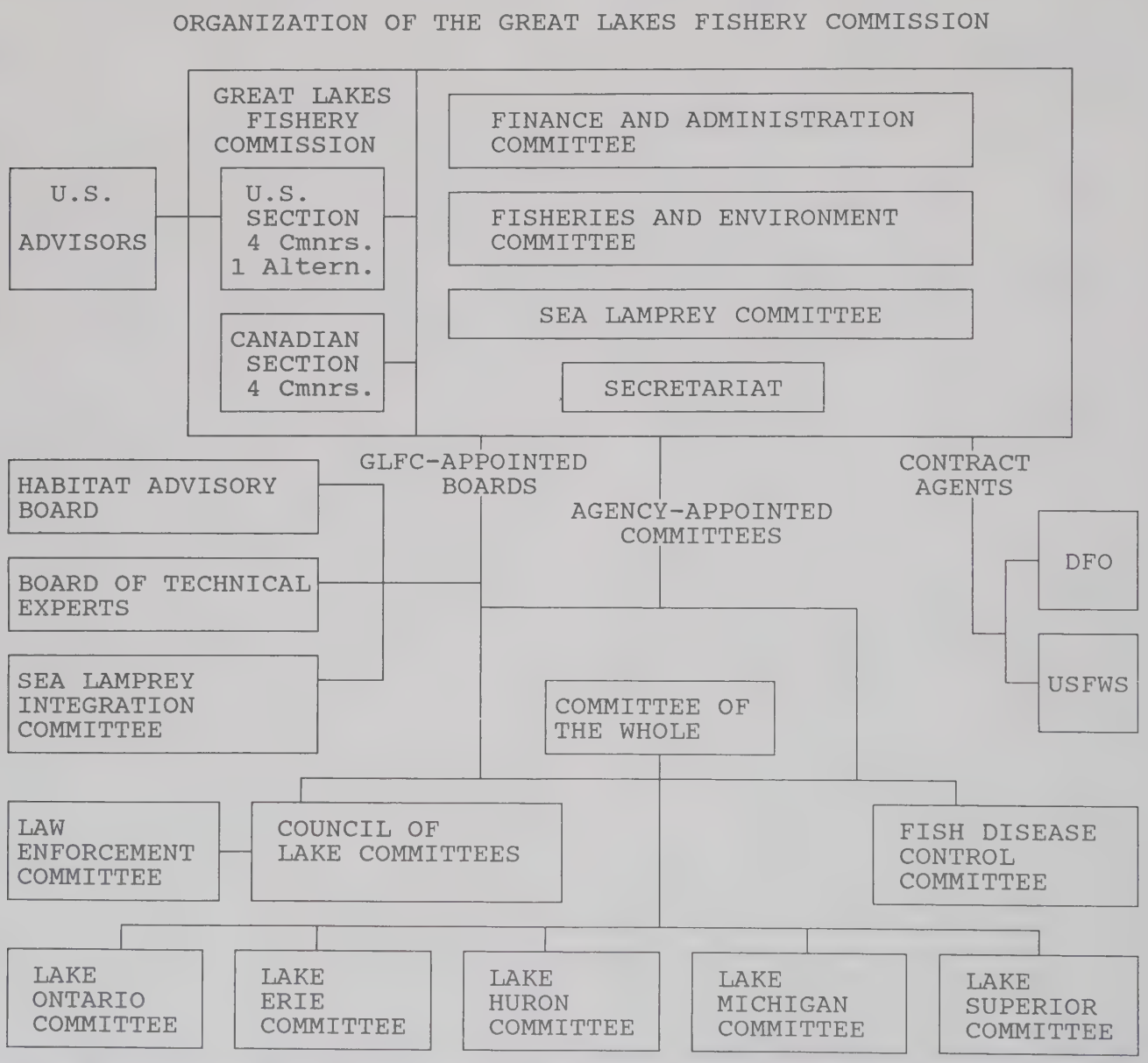

FIG. 1. The institutional structure of the Canada/U.S. Great Lakes Fishery Commission consists of Government-appointed Commissioners; staff or Secretariat; Great Lakes Governor-nominated, U.S. Commissioner-appointed citizen Advisors; Commission-contracted sea lamprey control agents; Commission-appointed Boards; and fishery agency-appointed committees.

Experts. Unpaid Commission appointees advise on policy and technical matters which may have been identified by either the Commission or the board itself. In addition, the Board of Technical Experts administers a small research program on behalf of the Commission.

Even more autonomous are the agency-appointed committees such as Lake Committees, the Fish Disease Control Committee, and the Law Enforcement Committee. These committees initiate and coordinate their own programs, with terms of reference from the Commission and broad direction from agency directors, for example through the 1980 Strategic Fishery Management Plan (GLFC 1980). Great Lakes fishery agency directors acting in concert are known as the Committee of the Whole. The Committee of the Whole is not truly under the Commission umbrella, since fish agency directors believe they can most effectively support and critique the Commission's program, when necessary, from an independent position.

Under U.S. legislation (Great Lakes Fisheries Act of 1956, Public Law 557 – 84th Congress) four advisors to U.S. Commissioners (U.S. Section) are nominated by State Governors for each of the Great Lakes under the state's jurisdiction, and appointed by the U.S. Section (U.S. Commissioners). The law encourages representation of recreational fishermen, the commercial fishing industry, the public at large, and the state fishery agency. The U.S. experience has been that not only are advisors a source of grassroots feedback, but they have also been appreciated supporters of Commission positions (eg. preventing ballast introductions) and programs (eg. sea lamprey control). The Canadian Section is currently arranging for its own formally appointed advisors.

Management of the Exotic Sea Lamprey

After thirty-five years, control of the exotic sea lamprey remains the major ongoing challenge for the Commission, and a constant reminder that potentially harmful introductions are more easily avoided than they are controlled. The opportunistic sea lamprey continues to challenge control technology and resources, for example by spawning in streams reclaimed from pollution and in secondary habitat in connecting channels (such as the St. Marys River).

The Convention's charge to "eradicate or minimize" sea lamprey numbers determined the Commission's approach in its first 25 years, within the limitations imposed by environmental and budgetary concerns. In 1957, a selective lampricide, 3-trifluoromethyl-4-nitrophenol (TFM), was discovered as the result of an intensive research effort (Applegate 1961). In the 1960's and 1970's sea lamprey populations were brought under control by the Commission's Agents, and lake trout were stocked by cooperating fishery agencies in an attempt to reestablish spawning populations decimated by the sea lamprey.

At the end of the 1970's, the Commission was introduced to the concept of integrated pest management (Sawyer 1980). Integrated pest management soon became the tool by which the Commission sought to reconcile ecological, social, and economic realities in its sea lamprey control program. Once simply "eradicate or minimize," current Commission objectives for the sea lamprey control program are:

1) to establish and achieve target levels of sea lamprey which permit the attainment and use of desired fish communities;
2) to minimize any negative impacts of the sea lamprey control program on the aquatic community, in particular through development and use of alternatives to chemical lampricides;
3) to further clarify rationale behind program requirements to Governments and allocation of benefits to managers and users of the resources.

Agency Forum for Controlling Spread of Fish Disease

Agency reliance on hatcheries to re-establish lake trout, and to provide fishing opportunities for anglers, brought associated risks of introducing diseases exotic to the Great Lakes and of increasing the incidence of those diseases already present. Fish agency pathologists, recognizing the need for cooperative action, organized themselves in 1973 under the Commission umbrella as the Great Lakes Fish Disease Control Committee. The successes of the Fish Disease Control Committee have prompted similar approaches on both coasts of North America.

By jointly stating their recommendations for responding to hatchery disease issues (often before such issues arise), pathologists have empowered their agencies to make sometimes unpopular but necessary decisions, such as destruction of seriously diseased hatchery fish. Fishery agencies acting in concert have also been able to observe a self-imposed 1978 ban on agency fish transfers from the West Coast (GLFC 1981), thereby denying Great Lakes access to the salmon disease IHNV (infectious hematopoietic necrosis virus) and most recently the rainbow trout disease VHS (viral hemorrhagic septicemia).

Briefly, the Fish Disease Control Committee's Model Program for Control of Fish Disease in the Great Lakes Basin (Hnath 1985) recommends that entire hatcheries rather than individual lots of fish be categorized based on regular inspections. A hatchery must pass three inspections over two years to be declared free of a disease. Diseases not found in the basin ("emergency diseases") are subject to the most stringent importation, transfer, and release requirements. The recommended response to diseases found in the basin ("restricted diseases") varies with disease severity, geographical isolation, and prospect for detection, treatment, or disinfection. Thus, whirling disease, whose spores persist in isolated areas of the Basin is subject to more severe requirements (no stocking until hatchery free of whirling disease for three annual inspections) than is the ubiquitous bacterial kidney disease (make every effort not to stock fish with overt BKD).

In support of the Model Program the Fish Disease Control Committee has issued recommended quarantine procedures (Horner and Eshenroder 1991) for use by agencies wishing to import new strains or broodstocks from outside the Great Lakes Basin. Although concerns remain for West Coast imports, the Committee accepts that tradeoffs between genetics and disease are necessary to meet certain management needs, especially in rehabilitating lake trout. The Committee's quarantine guidelines are an attempt to meet legitimate management needs without also introducing diseases exotic to the Basin.

In the future the Fish Disease Control Committee is expected to attend to the needs of private aquaculture, whose activities have the potential to quickly nullify agency gains in disease control. For example, because sources of rainbow trout eggs east of the continental divide are insufficient in quantity for private sector needs, the private sector imports from those IHNV-enzootic areas that the agencies avoid. Also, in many areas of the Basin reliable, reasonably priced diagnostic services are not available to smaller private operators, who thus

find it impossible to comply with the Model Program, regardless of intentions. Another obstacle to private sector cooperation is the absence of compensation when serious disease warrants destruction of all fish onstation.

Finally, the Fish Disease Control Committee is aware that regulations pertaining to exotics and disease vary by jurisdiction in effectiveness. Such variation causes inefficiencies in both private aquaculture and in the enforcement of regulations. Of all the Great Lakes states only Minnesota bans private importation of eggs from the West Coast where IHNV is endemic.

Champion for Conserving Native Genetic Resources

Caution in adding exotic species to the Great Lakes has as its objective the protection of the existing diversity and productivity of the aquatic community, as well as protection of users of the resource (Eshenroder 1989). In the 1970's the Commission (in particular the late Ken Loftus) became concerned that the existing genetic diversity of species native to the Great Lakes was being threatened by man's activities. In 1980 the Commission sponsored the Stock Concept Symposium, which had among its objectives, development of strategies for preserving native gene pools in fish culture and in other management activities (Berst and Simon 1981).

Subsequent to the Stock Concept Symposium, the Commission published guidelines for managers seeking to protect genetic diversity in the stocks they managed (Berst and Spangler 1983; Kapuscinski and Jacobson 1987). In the early 1980's the Commission-sponsored Conference on Lake Trout Research charted new research directions / priorities for preserving native lake trout strains for use in rehabilitating this species in the Great Lakes (Eshenroder et al. 1984). Many of these concepts underlie broodstock strategies in lake trout rehabilitation plans being developed cooperatively for each of the lakes by fishery management agencies.

Forum for Interagency Consultation and Cooperation in Managing Fish Intoductions

The perturbation of existing communities by pollution, overharvest, and by invaders such as sea lamprey and alewife (Emery 1985) opened and created niches which fishery managers were tempted to fill (Tody and Tanner 1966), both to provide new fishing opportunities and to restore stability. Fish agencies soon came to appreciate the benefits of consulting one another before taking often unrevokable steps such as the introduction of striped bass and grass carp. Consultations were formalized in 1980 when agency directors, operating under the Commission umbrella, adopted "A Joint Strategic Plan for Management of Great Lakes Fisheries" or SGLFMP (GLFC 1980). Tribal management authorities adopted SGLFMP in the mid-1980's. "Invasion and introduction of exotic species" was prominent among the fisheries issues identified in SGLFMP. Agency directors agreed that:

> "Consensus must be achieved when management will significantly influence the interests of more than one jurisdiction,"

and that

> "If consensus cannot be received with respect to fish community objectives an affected party may request a hearing before the Great Lakes Fishery Commission which will arbitrate such differences, report its findings, and make recommendations for resolution of the problem to the appropriate agencies."

To date agencies have referred but one issue to the Commission. In 1986 the Commission ruled that evidence available at the time did not warrant destruction of hatchery lake trout now thought to have been infected with the previously unknown disease epizootic epitheliotropic disease virus or EEDV (McAllister and Herman 1989).

In 1987, representative fish managers, pathologists, and advisors recommended that an introductions policy be developed for adoption by agency directors (GLFC 1987). This policy would formally support agency objectives for fish communities and the biological integrity of the Great Lakes. It would also formalize consultation procedures for agency introductions, and attempt to focus public and legislative attention on the risks associated with ill-considered introductions. Managers were particularly concerned at the time with the inadequacy or regulations in regulating both the movement of fish and water by the burgeoning private aquaculture and baitfish industries. Progress on the draft policy and consultation procedures was interrupted in 1988, when ballast water introductions emerged as a more immediate priority.

In support of agency efforts to manage introductions by both private and public sector, the Commission has sponsored and published analyses of aquatic organisms introduced into the Great Lakes including modes of entry. In his review of fish introductions during the period 1819 – 1974 Emery (1985) found that half of the 34 introduced fish species became established in the Great Lakes. A more recent analysis reported 127 exotic plants, animals, and disease agents as established in the Great Lakes. One third of these introductions were attributed to ballast water (Leach and Lewis 1991).

Proponent for Preventing Ballast Introductions

The last two years have seen the Commission take an activist role in a manner envisaged by both the 1955 Convention and the Joint Strategic Plan for the Management of Great Lakes Fisheries. The latter stated that:

> "Unresolved environmental issues may be referred by lake committees to the Great Lakes Fishery Commission which shall represent fishery interests in these issues to the most appropriate body (eg. International Joint Commission, United States Environmental Protection Agency, United States State Department, Canada Department of External Affairs, etc.)."

In 1988, a European percid, ruffe (*Gymnocephalus cernuus*), was reported in Duluth Harbor in western Lake Superior, apparently discharged with the ballast of oceangoing vessels. Fish managers urged the Commission (GLFC 1988a, GLFC 1988b) to press Governments for measures to prevent additional such introductions. This recommendation acquired additional weight a few months later with the report of European zebra mussels (*Dreissena polymorpha*) in Lake St. Clair, also attributed to oceangoing vessels (Hebert et al. 1989).

The Fishery Commission brought the ballast introductions problem to the attention of the Canadian Department of External Affairs and the American State Department in August of 1988 (as did the International Joint Commission). Mid-ocean ballast exchange was proposed as a cost-effective and quickly-implemented preventive strategy (IJC and GLFC 1990). Governments were reminded of a previous agreement which called upon the Coast Guards of the two countries to study the prob-

lem, as well as possible remedies, of organism transfer in the ballast of oceangoing vessels (Annex 6 of the Great Lakes Water Quality Agreement of 1978 as amended by Protocol, signed November 18, 1987).

Decisive progress has been made since the two Commissions raised the issue of ballast introductions with the Governments: (1) (voluntary) Great Lakes Ballast Water Control Guidelines, implemented by the Canadian Coast Guard 1 May 1989; (2) 1989 self-reported compliance with Canadian Guidelines of 83% (Tom Fleck, Canadian Coast Guard, Ottawa, personal communication); (3) a 1990 Canadian Coast Guard-sponsored study on the effectiveness of the ballast exchange strategy and compliance with the Canadian Guidelines; (4) a U.S. Congressional request for a Coast Guard report on options available for preventing introduction of viable organisms with discharge of ballast water from ballast of oceangoing vessels (P.L. 101-225); (5) U.S. legislation requiring ballast exchange or treatment of all ocean-going vessels entering the Great Lakes (P.L. 101-646, Non-indigenous Aquatic Nuisance Prevention and Control Act of 1990); and (6) establishment of a ballast work group by the Marine Environment Protection Committee of the United Nation's International Maritime Organization, effective November 1990.

However, the two Commissions remain concerned as in 1990 two new species of goby from the Caspian Sea (*Proterorhinus marmoratus, Neogobius melanostoma*) were reported for the first time in the St. Clair River which drains Lake Huron (David Jude, U. of Michigan, 2200 Bonisteel Blvd., Ann Arbor, MI 48109, pers. comm.). In October 1990 the International Joint Commission, and the Fish Commission submitted a joint report to Governments, urging that all oceangoing vessels exchange or treat ballast water before discharging same in the Great Lakes and connected waters, and that ecologically compatible alternatives to ballast exchange be developed (IJC and GLFC 1990).

More effort is needed in order to protect the Great Lakes from continued inoculations of exotic organisms with ballast water. The 83% compliance rate must be increased to 100% – partial discharge of the thousands of cubic meters of unexchanged or untreated ballast water carried by one ship is sufficient to effect an introduction. No less importantly, ships calling in contiguous waters such as the lower St. Lawrence and the Hudson Rivers must also exchange or treat their ballast – exotic species introduced to North America in ballast water, such as the cladoceran *Bythotrephes cederstroemi*) and the zebra mussel (*Dreissena polymorpha*) are capable of invading the Great Lakes if first established in the Hudson or St. Lawrence Rivers.

Management of Ballast-Introduced Aquatic Organisms

The Commission has thus far taken a supporting role in responding to recent arrivals ruffe and zebra mussel, both of which have potential for transforming existing fish communities (Maitland and East 1989; Mackie et al 1989; Pratt 1988; Pavlovskuj and Sterligova 1986; Bergman 1988). Prior to advising Governments in 1988 of potential for harm, the Commission sponsored a study to determine the range and numbers of the ruffe in Lake Superior's Duluth Harbor (Pratt 1988), and provided a forum for managers to debate whether eradication efforts should be undertaken (GLFC 1988).

Although in 1988 ruffle eradication was not believed to be feasible in the St. Louis River (Duluth Harbor), potential predators of the ruffe were stocked in the St. Louis River and angling restrictions were introduced. Managers in Minnesota and Wisconsin prohibited possession of ruffe in order to deter the species' spread inland, for example as baitfish. Fish agencies also sought the Commission's assistance (GLFC 1990) in convincing lake vessels calling at Duluth Harbor to avoid ballasting in the St. Louis River and nearby Lake Superior when young ruffe are present (end of May through July). Managers hope that the cold waters of Lake Superior will continue to inhibit the Great Lakes invasion of ruffe, granting an interval to learn from the St. Louis River experience with the species. A more formal review of management options was initiated by the Commission in May 1991.

As mentioned previously, the Commission's mandate limiting it to issues affecting Great Lakes fish stocks of common concern was insufficiently comprehensive to permit the Commission to assume responsibility for coordinating management of the zebra mussel. Thus the Commission has taken some preliminary steps to ensure that fishery issues are not overlooked in favour of pipeline blockage issues. It carefully follows the work of the many independent researchers for evidence of harm to "fish stocks of common concern." The Commission has asked its Board of Technical Experts to issue a list of fisheries research priorities for reference by independent funding agencies, in addition to a planned analysis of the reasons for the Great Lakes' apparent "vulnerability to invasion." Also the Commission has taken every opportunity from testifying for the U.S. Congress to addressing professional gatherings and granting press interviews, to advise governments, the public, and basin researchers on the advisability of containment measures in the lab, on boat hulls, and in the bait bucket. The pet and garden trade should be prohibited from spreading the zebra mussel throughout North America.

Conclusion

The Commission's mandate has served the Great Lakes well in preventing, controlling, and managing exotic introductions. The Commission has represented fishery interests outside its usual circle of cooperators, as with ballast introductions. It has provided a forum for fishery agencies to coordinate their own activities in a responsible fashion, championed the conservation of genetic diversity native to the Great Lakes, and controlled the exotic sea lamprey to levels which permit fishery agencies to attain their fish community objectives. We hope that Governments and Great Lakes managers will continue to see the Commission as an important ally in conserving and protecting the previous genetic resources of the Great Lakes aquatic community, as well as protecting the interests of today's users and those who will follow.

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Synthesis and Recommendations

Ecological and Genetic Effects of Fish Introductions: Synthesis and Recommendations[1]

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Allendorf, F. W. 1991. Ecological and genetic effects of fish introductions: synthesis and recommendations. Can. J. Fish. Aquat. Sci. 48 (Suppl. 1): 178–181.

The papers resulting from this symposium review the ecological and genetic effects of fish introductions throughout the world. Purposeful introductions rarely have achieved their objectives. Moreover, both intentional and unintentional introductions usually have been harmful to native fishes and other taxa through predation, competition, hybridization, and the introduction of diseases. We must learn from the past in order to avoid mistakes in the future. Introductions should not be used as a management tool without sufficient prior information and understanding to predict their effects. Introductions are often made or permitted because of the demands of certain interests groups (e.g., anglers or aquaculturists). Education of the public to the potential dangers and costs of such introductions is essential. Cooperation among management agencies is necessary to regulate and control both the purposeful and accidental introductions of fishes.

Les articles rédigés à la suite du présent symposium passent en revue les effets écologiques et génétiques de l'introduction de poissons dans le monde. L' introduction intentionnelle a rarement atteint ses objectifs. De plus, l' introduction, intentionnelle ou non, a en général été néfaste pour les poissons indigènes et pour d'autres taxons à cause de facteurs comme la prédation, la compétition, l'hybridation et l' introduction de maladies. Il faut tirer une leçon des erreurs passées pour éviter d'en commettre de nouvelles. L' introduction ne doit pas être utilisée comme outil de gestion sans qu'on ait au préalable des renseignements suffisants pour en prévoir les effets. L'introduction est souvent réalisée ou autorisée pour répondre à la demande de certains groupes d'intérêts (c.-à-d., les pêcheurs ou les aquiculteurs). Il est essentiel d'informer le public sur les dangers et les coûts possibles de l' introduction. Il est nécessaire que les organismes de gestion coopèrent pour réglementer et surveiller l' introduction de poissons intentionnelle et accidentelle.

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The previous papers from this symposium do a thorough job of documenting and discussing the ecological and genetic effects of fish introductions throughout the world. They also present an overview of existing regulations that govern fish introductions in Canada and the United States. My task is to synthesize these papers and to present recommendations coming from this symposium that will provide guidance to fisheries managers.

The term introduction is used here in the broad sense. That is, any intentional or accidental release of fish by humans into the wild is considered an introduction. Some of the papers in this symposium (e.g., Holčík 1991; Krueger and May 1991) have used a more narrow meaning that limits introductions to release of fish into waters outside of their native or original range. The more general meaning of introduction is used here because many of the papers in this symposium deal with the release of fish within their native range, and because many of the biological and legal aspects apply equally to introductions inside and outside of the native range of a species.

This broader definition of " introduction" is in agreement with the terminology adopted by the Exotic Fish Section of the American Fisheries Society (Shafland and Lewis 1984). They define "introduced" as any plant or animal moved from one place to another by humans. They also point out that no terms have been used consistently to identify introductions of individuals within the native range of a species. Ferguson (1990) has adopted the terminology of Shafland and Lewis (1984) and suggested that the term "transfers" be used to signify introductions within the native range of a species.

Many comprehensive reviews of the effects of fish introductions have appeared in the last several years (Courtenay and Stauffer 1984; Holčík 1984; Moyle 1986; Welcomme 1988; Baltz 1991; Ross 1991). This symposium differs from previous overviews because of the emphasis on genetic concerns. The genetic effects of introductions are often more difficult to detect and monitor than are demographic or ecologic effects (Marnell 1986; Ferguson 1990). Nevertheless, several papers in this symposium show that genetic effects of introductions constitute a threat to the long-term existence of many wild populations and species (Billington and Hebert 1991; Krueger and May 1991; Philipp 1991; Waples 1991).

Effects of Introductions

It is difficult to evaluate the success of introductions for a variety of reasons. A primary problem is that introductions are often made without appropriate mechanisms to evaluate if the desired objective is achieved (Holčík 1991; Philipp 1991). In addition, those evaluations that have been done often ignore possible effects of introductions on other taxa such as native

[1]This paper forms part of the Proceedings of the Ecological and Genetic Implications of Fish Introductions Symposium (FIN) convened at the Great Lakes Institute, University of Windsor, Ontario, Canada, May 17–19, 1990.

fishes, amphibians, and invertebrates (Arthington 1991; Holčík 1991; Wingate 1991). To compound these problems, exaggerated and undocumented claims of success are often made by those responsible for introductions (Holčík 1991; Philipp 1991).

The geographical and temporal scale of comparison used to evaluate introductions also presents a variety of problems. For example, in many cases introductions have increased the number of species existing within particular geographical or political areas. Viewed on this narrow scale, introductions may appear to increase biodiversity. However, such introductions also have caused the extinction of many species. Thus, on a global scale introductions have reduced biodiversity.

For example, California's Clear Lake, one of the oldest lakes in North America, contained 12 native species of fish (Moyle 1986). Today there are 23 species of fish in Clear Lake. However, five of the native species have been extirpated, and two of these are globally extinct. The 16 introduced species are abundant in many places throughout the world. Thus, Clear Lake has a more diverse fish fauna today, but the world has two fewer species of fish (Moyle 1986).

The temporal scale is also important to consider. Any beneficial effects of introductions usually occur immediately while the harmful effects are often delayed. Thus, we are often faced with political and economic pressure to embrace short term benefits at the cost of the long term well-being of an ecosystem (Philipp 1991).

Most harmful effects of introductions are irreversible (Dochoda 1991; Philipp 1991). Thus, we are facing a ratchet effect. The incremental loss of biodiversity in a political time scale through loss of populations, subspecies, and species may seem to be an acceptable cost in each individual case. However, gradual but continual decay will lead to disastrous losses of biodiversity in the long term.

Another difficulty of scale in evaluating introductions is the units with which we measure success or failure. The desired benefits of introductions are usually some short-term aspect of human well-being (e.g., food or recreation) or profit (e.g., commercial fishery or aquaculture). The overall effect of such introductions often involves these two measures balanced against a loss in biodiversity. This is a difficult balance to evaluate (Ehrenfeld 1976). For example, how much money is a species of fish worth? How about an endemic invertebrate species?

Several papers in this symposium review the history of fish introductions on all continents of the world except Antarctica (Arthington 1991; Crossman 1991; Fernando 1991; Holčík 1991; Ogutu-Ohwayo and Hecky 1991). These papers indicate that most introductions have not been successful. That is, most purposeful introductions have not achieved their objectives. More importantly, any benefits of introductions have come at considerable costs; most introductions, both intentional and unintentional, have had a harmful effect on native fish and other taxa through predation, competition, hybridization, and the introduction of diseases.

The papers in this symposium deal largely with freshwater systems. A recent review of introduced fishes in marine systems and inland seas (Baltz 1991) supports the conclusions drawn by the papers in this symposium. Most intentional introductions in marine ecosystems either have not achieved their objectives or have had harmful effects on native species. In several cases, introduced marine species contributed to the extinction of native species.

Individual Recommendations

Two types of recommendations emerged from the workshop. Many of the individual papers make recommendations relevant to their specific topic. Recommendations also emerged from the group discussion at the end of the meeting. This section reviews and synthesizes the recommendations made in the individual papers.

Doyle et al. (1991) recommend that aquaculture breeding programs should be designed to develop numerous stocks specially adapted to local environments. This may minimize genetic impact of aquacultural stocks on wild stocks while producing economic benefits for individual farmers and conserving the genetic variation among stocks that is necessary for continued successful culture over a longer time-scale.

The potential problem of the accidental release of aquacultural stocks is demonstrated by their example of Atlantic salmon (*Salmo salar*) in Norway. Currently, about 70% of the Atlantic salmon farmed in Norway come from a single breed developed at the Institute of Aquaculture Research (Doyle et al. 1991). The number of escaped fish from these operations increased dramatically throughout the 1980's. For example, an estimated 1.2 million salmon escaped from Norwegian fish farms during storms in December 1988 and January 1989 (Hindar et al. 1991); these accidental releases are equivalent to the total annual catch of wild Atlantic salmon in Norway.

Stewart (1991) recommends actions to control disease organisms and pests associated with introductions. He believes that inspection and certification programs must be initiated and guided by national and international regulations. He also emphasizes the importance of research facilities so that the threats of introductions can be understood and minimized.

Holčík (1991) does a thorough job of reviewing the history of fish introductions into European waters. He points out that generally we lack the information needed to judge the overall success of such introductions. The success of introductions is often exaggerated while the adverse effects are ignored. He recommends the international acceptance of the Code of Practice adopted by the European Inland Fishery Advisory Commission in 1987 to regulate and control fish introductions.

The remaining individual recommendations come from the papers in the symposium that dealt with the genetic effects of introductions. Kapuscinski and Hallerman (1991) consider the potential effects of the introduction of transgenic fish into natural ecosystems. They believe that performance evaluations of transgenic fish are essential to gain insight into their potential ecological impacts. They recommend that stocking of transgenic fishes in natural waters should be opposed and that their use in aquaculture should be restricted.

Philipp (1991) considers the long term consequences of introducing Florida largemouth bass (*Micropterus salmoides*) into the native range of northern largemouth bass. His results indicate that such introductions are likely to cause the loss of native locally adapted populations and to reduce the value of the local fishery by hybridization. He cautions that introduction programs that will result in hybridization between different stocks should be recognized as irreversible actions. Therefore, such programs should not be undertaken until it is known that the genetic changes of the recipient populations will not lead to irreparable damage.

Evans and Willox (1991) provide an interesting complement to the recommendations of Philipp. They consider the effects of stocking hatchery-reared lake trout (*Salvelinus namaycush*)

into waters containing native populations. In contrast to Philipp, however, they do not consider the effects of hybridization between the introduced and native fish. Nevertheless, they conclude that the introduction of hatchery-reared trout can result in the rapid loss of the native stock because of increased exploitation, even in the absence of reproduction of the introduced fish! They recommend that emphasis needs to be placed on protection of wild stocks, and that supplemental introductions into these populations should be terminated until the potential effects are known.

Krueger and May (1991) echo the concerns of Philipp, Evans, and Willox in their review of introduction of salmonid fishes. They feel that supplemental stocking is appropriate for rehabilitation programs only where wild fish are threatened or extinct. They recommend that non-native salmonids should not be introduced where wild native salmonid populations now exist. They also emphasize the importance of developing policies to deal with the risks presented by releases of fish by the aquaculture industry and by the release of genetically engineered fishes.

Waples (1991) reviews the history of genetic interactions between hatchery and wild salmonids in the Pacific Northwest of the United States. He concludes that supplementation programs have not been successful and that such programs present a threat to the long term survival of Pacific salmon species. He suggests that the rule of supplementation programs should be "first, do no harm." That is, such programs should not be undertaken unless there is adequate assurance that wild stocks will not be harmed. He also recommends that monitoring programs should be an integral part of any supplementation effort.

Group Recommendations

A lively discussion at the end of the meeting served to focus the views held by the participants. The consensus was that introductions generally have been harmful. That is, our fisheries resources and our natural ecosystems throughout the world would be in better shape today if fish introductions had not been a common tool of fish management agencies over the last century.

Most of the group discussion dealt with what should be done in the future. Group recommendations for future actions were developed in four different categories of activities.

1. Education
2. Cooperation
3. Regulation
4. Research

Education is a key in dealing with these issues. Many of the past and current arguments in favor of introductions have been based upon perceived societal demands for food, recreation, or economic benefits. There are two central educational issues. First, the history of introductions tells us that such introductions rarely achieve their objectives (Arthington 1991; Holčík 1991; Wingate 1991). Second, society must realize that such introductions also involve a "cost" and we usually do not understand natural systems sufficiently to know what the cost will be. There needs to be increased effort to educate the public and management agencies on the limitations and dangers of fish introductions (e.g., Goodman 1991).

Cooperation among management agencies is essential. Unfortunately, management objectives and responsibilities usually are defined upon political rather than geographical or biological boundaries. Ecosystems are not constrained by political boundaries. Management agencies must consider the potential long term effects of introductions inside and outside their areas of geographical and taxonomic responsibilities. Such organizations as the Great Lakes Fisheries Commission should play a bigger role in making management decisions rather than allowing individual provinces or states to pursue their own agendas that are sometimes in direct conflict with one another. Management actions are also sometimes hampered by institutional constraints arising from conflict between federal and local jurisdiction (Thompson 1974).

Regulations and policies should be developed and enforced that recognize and encourage cooperation among responsible agencies to protect natural ecosystems. It was pointed out that there is some danger of reinventing the wheel in this regard. A variety of regulations already exist (Leach and Lewis 1991; Stanley et al. 1991; Wingate 1991). In addition, many groups of scientists have already published recommended policies in these areas (e.g., Anonymous 1981; Berst and Spangler 1983). Rather than publishing more lists of recommended policies we need to recognize and implement existing recommendations and enforce existing regulations.

Research was identified as the fourth area of critical need. We need to be able to better anticipate the effects of proposed introductions. This is an especially critical need because little effort has been spent in the past evaluating the effects of introductions (e.g., Holčík 1991; Philipp 1991). Participants agreed that we need to follow the rule suggested by Waples (1991): "First, do no harm." That is, introductions should not be undertaken unless there is adequate assurance that wild stocks of fish and other species will not be harmed.

Acknowledgments

This paper is dedicated to Phil Pister, Executive Secretary of the Desert Fishes Council, on his retirement from the California Department of Fish and Game shortly before this meeting; Phil's enthusiasm and dedication are an inspiration to us all. I thank Kathy Knudsen, Robb Leary, and Phil Pister for their helpful comments on this manuscript, Paul Hebert and Neil Billington for giving me the challenge of synthesizing contributions to the symposium, Lisa Seeb for providing me with detailed notes from the group discussion at the meeting, and J. Holčík for sending me relevant papers.

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